

The Pathogenicity and Seasonal Development of Gymnosporangium in Iowa

BY DONALD E. BLISS

AGRICULTURAL EXPERIMENT STATION
IOWA STATE COLLEGE OF AGRICULTURE
AND MECHANIC ARTS

R. E. BUCHANAN, Director

BOTANY AND PLANT PATHOLOGY



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SUMMARY

Seven species of the genus *Gymnosporangium* occur in Iowa, but only *G. juniperi-virginianae*, causing cedar-apple rust, and *G. globosum*, causing hawthorn rust, are common. The latter is of little economic importance.

The epidemic of cedar-apple rust in 1928 caused an estimated loss of \$200,000 in Iowa.

Six to seven hours were required to produce abundant sporulation from air dry galls of *G. juniperi-virginianae* regardless of whether the period of soaking was 30 or 180 minutes.

Newly-matured aecidiospores of *G. juniperi-virginianae* germinated to the extent of 54 percent in July. A lot was divided and the percentage of germination in the portion refrigerated at 5 to 13°C. increased rapidly for at least 22 days, while that in the portion held at room temperature for the same interval dropped to zero.

At Shenandoah the interval between infection and first opening of aecidia of cedar-apple rust on Bechtel's flowering crab was about 72 days. That for hawthorn rust on *Crataegus mollis* was about 81 days.

Seedlings of red cedar were successfully inoculated using aecidiospores of *G. juniperi-virginianae*. Large differences in the number of galls on trees which had received similar treatments suggested a variation in disease resistance.

The only appreciable germination of aecidiospores of *G. globosum* was obtained in November from diseased hawthorn leaves which had fallen to the ground and others which were refrigerated 41 days at 5°C.

Differences in the degree of maturity reached by the cedar rusts are utilized in defining the relative susceptibility of their aecidial hosts.

The percentage of leaf area covered by lesions of cedar-apple rust is recorded for 138 varieties of apples and 28 varieties of crabapples which were growing in nursery rows at Shenandoah during the years, 1928 to 1930. Aecidiospores were matured on only 30 percent of these hosts.

The percentage of infected apple leaves seemed to vary roughly as the percentage of diseased leaf area, but leafiness was not related to the amount of rust infection. These lines of evidence suggest that the period of susceptibility in leaves of susceptible varieties may be longer than that of resistant ones.

Artificial inoculations show that Tolman and York Imperial varieties of apple are very susceptible to the strain of *G. juniperi-virginianae* from Morgantown, W. Va., but are resistant to other strains from Ames and Shenandoah, Iowa; Manhattan, Kan., and Cochrane, Wis. The results indicate the presence of physiologic specialization within the species. There is little evidence that the susceptibility of trees of one variety of apple may vary in different sections of the country.

None of the observed varieties of apple or crabapple seem to be susceptible to *G. globosum* in Iowa.

The Pathogenicity and Seasonal Development of *Gymnosporangium* in Iowa¹

By DONALD E. BLISS²

Because cedar-apple rust can be controlled successfully only by the isolation of apples from red cedars, this fungous parasite represents a peculiar problem in Iowa where both of its hosts are trees of value. The red cedar, *Juniperus virginiana* L., is the only widely distributed native conifer in Iowa. It is also cultivated commonly for shelterbelts, and its numerous horticultural varieties, because of their rare beauty, are utilized by the landscape gardener. Seventy percent of the 2,840,000 apple trees in Iowa are in home orchards. The red cedar is often used as a shelterbelt for the orchard or for esthetic purposes in the landscaping of the farmstead. Where orcharding is practiced commercially, however, the rust damage becomes a real economic problem not to be solved individually, because cedar-apple rust does not yield to orchard spraying. The severe epidemic in 1928 in the commercial orchards in western Iowa prompted the orchardists to seek legislation in 1929 that would make it possible to eradicate red cedars in and about commercial orchards; a program involving local voluntary cooperation in replacing the red cedars in the Harrison County district and an investigation of the cedar-apple rust problem was initiated in the state. It was soon apparent that more information was needed regarding the relationship, prevalence and distribution of all the cedar rust fungi in Iowa.

Host ranges of cedar rusts were poorly defined, and many conflicting statements were found regarding the relative susceptibility of the known hosts, especially in the case of *Gymnosporangium juniperi-virginianae* on varieties of cultivated apple. The seasonal development of *G. juniperi-virginianae* and *G. globosum* under Iowa conditions was only imperfectly understood, and the susceptibility of different species of *Juniperus* warranted consideration. This bulletin contains data tending to clarify many phases of these problems for Iowa conditions.

¹ Taken from a thesis submitted to the faculty of the Graduate College, Iowa State College, in partial fulfillment of the requirements for the degree, doctor of philosophy. Project No. 82 of the Iowa Agricultural Experiment Station.

² The author hereby expresses his sincere appreciation to Dr. I. E. Melhus for the direction of the work and generous assistance in preparation of the manuscript, to Dr. J. C. Gilman for useful advice, and to the Mount Arbor and Shenandoah nurseries, Shenandoah, Iowa, for cooperation and many courtesies.

THE SPECIES OF GYMNOSPORANGIUM IN IOWA AND
SEASONAL DEVELOPMENT OF *G. JUNIPERI-
VIRGINIANAE* AND *G. GLOBOSUM*

The object of this chapter is to summarize the present knowledge of the occurrence of the genus *Gymnosporangium* in Iowa and to report recent experiments dealing with the life history and biology of the rusts of the common apple and hawthorn.

THE SPECIES OF GYMNOSPORANGIUM IN IOWA

Arthur (5,7), Pammel (38,39), Wilson (58) and Kern (35) have contributed much to our knowledge of the genus *Gymnosporangium* as it occurs in Iowa. This paper reports observations of the cedar rust fungi in Iowa and gives illustrations of four species, and notes regarding host range, distribution and economic importance.

GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE SCHW.

This species is common throughout Iowa and is the most important economically because of its ability to seriously weaken both the cultivated apple and the common red cedar. (Figs. 1 and 2.)

Host plants in Iowa: *Pyrus malus* L., *P. ioensis* (Wood) Bailey, *P. ioensis* var. *plena* Rehd. (Shenandoah, 1928), *Juniperus virginiana* L., *J. virginiana* var. *glauca* Carr. (Charles City, 1929), *J. virginiana* var. *canaertii* Senecl. (Charles City, 1929), *J. virginiana* var. *elegantissima* Hochst. (Ames, 1928; Shenandoah, 1929), *J. virginiana* var. *schottii* Gord. (Shenandoah, 1928; Ames, 1928), *J. virginiana* var. *hillii* Hort. (Ames, 1929), and *J. scopulorum* Sarg. (Hampton, 1929; Charles City, 1929; Des Moines, 1929; Ames, 1930).

The herbarium of Iowa State College contains a specimen of rust on *Crataegus mollis* (T. and G.) Scheele collected by E. B. Watson at Columbus Junction, 9-10-02, which is referred to *G. juniperi-virginianae* Schw.; a doubtful determination, since the rust is similar to *G. globosum* Farl.

Pammel (39) shows figures of the aecidia of *G. juniperi-virginianae* [*Roestelia pyrata* (Schw.) Thax.] on *Crataegus bipinnatifida* and Mercer crab (*Pyrus ioensis*). The aecidia on *Crataegus* are depicted as long, tubular and lacerate, while those on Mercer crab have distinctly recurved peridia. There are also noticeable differences in the size, form and markings of the peridial cells. Pammel says, "In *Crataegus punctata* as well as in *Crataegus mollis* the peridial cells extend much (farther) . . . beyond the surface of the leaf, and they are more finely lacerate. In the *Pyrus Iowensis* (*P. ioensis*) the cups are shorter, darker brown, and the peridial cells do not cling together as in (*Crataegus* spp.) . . . In the cultivated apple the cups are much smaller than (those on) either of the other host plants. They

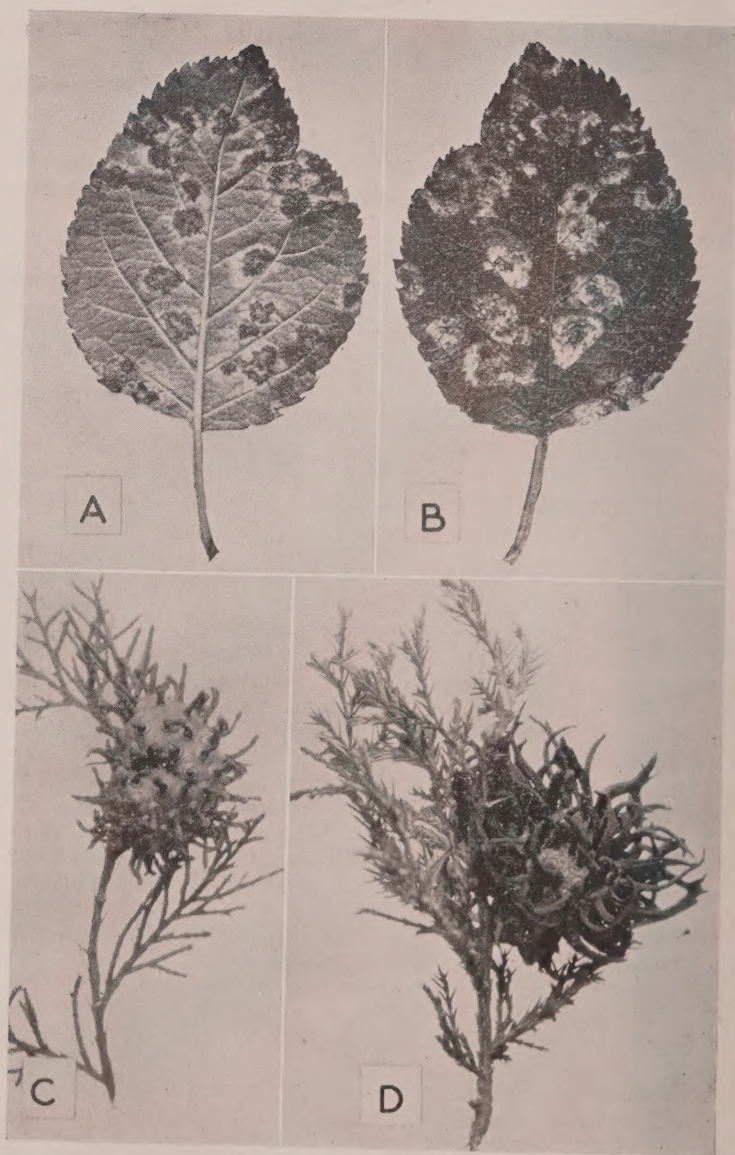


Fig. 1. *Gymnosporangium juniperi-virginianae*. A. Aecidia on lower surface of leaf of Jonathan apple. B. Upper surface of same leaf showing pycnidia. C. Gall on twig of red cedar with teleutospores before wetting. D. A similar gall showing teleutospores after soaking in water.

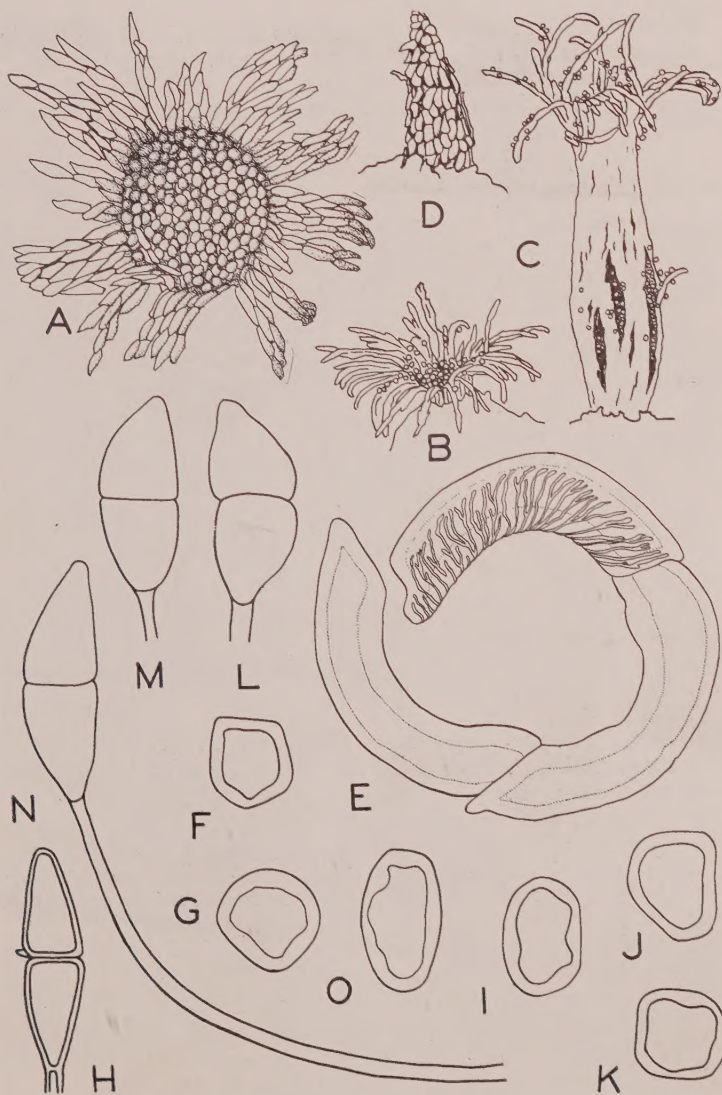


Fig. 2. *Gymnosporangium juniperi-virginianae*. A. An open acedidium containing many aecidiospores. In this position the strips of peridial cells allow the aecidiospores to escape, but when wet, they curl inward and close the mouth of the acedidium. X60. B. An acedidium from which most of the aecidiospores have escaped. X43. C. Side view of a mature acedidium. Strings of peridial cells are splitting downward thus allowing the aecidiospores to escape. X43. D. The pointed tip of a young acedidium which has pierced the epidermis of the leaf. X43. E. Three peridial cells in side view showing inward curvature when wet. The irregularly-branched figures on one of the cells represent the ridges which mark the inner and side walls. X518. F, G, O, I, J, K. Aecidiospores. X518. L, M, N, H. Teleutospores. X518.

project (only) . . . slightly beyond the surface." Since the description of aecidia of rust on *Crataegus* spp. corresponds closely to *G. globosum*, while the rust on the wild crab and cultivated apple is like *G. juniperi-virginianae*, the question arises whether Pammel was not confusing two species.

GYMNOSPORANGIUM GLOBOSUM FARLOW

Although it is common throughout Iowa, at present *G. globosum* is of only slight economic importance. It reduces the vitality and ornamental value of its hosts. Should it become common on *Pyrus communis* or on the cultivated apple, as it is in New York and Indiana, it will present a problem similar to that of *G. juniperi-virginianae*. (Figs. 3, 4 and 5.)

Host plants in Iowa: *Crataegus margaretta* Ashe, *C. mcgeae* Ashe, *C. mollis* (T. and G.) Scheele, *C. per-tomentosa* Ashe, *C. punctata* Jacq., *C. rotundifolia* Moench., *C. tomentosa* L., *Pyrus communis* L. (Kent, 1930), *Juniperus virginiana* L., *J. scopulorum* Sarg.

Because of the complexities in the genus *Crataegus*, no attempt has been made to identify all of the numerous species in Iowa which serve as hosts.

The following rusts are comparatively rare in Iowa and hence of no economic importance at present.

GYMNOSPORANGIUM GERMINALE (SCHW.) KERN

Host plants in Iowa: *Crataegus monogyna* Jacq., (Oskaloosa, 1927) *Juniperus virginiana* L.

GYMNOSPORANGIUM CLAVARIAEFORME (JACQ.) DC.

Host plants in Iowa: *Amelanchier spicata* (Lam.) C. Koch, *Juniperus communis* L.

GYMNOSPORANGIUM NIDUS-AVIS THAXTER

Host plants in Iowa: *Amelanchier canadensis* (L.) Medic., *Juniperus virginiana* L.

GYMNOSPORANGIUM CORNICULANS KERN

Host plant in Iowa: *Amelanchier canadensis* (L.).



Fig. 3. Lesions with pycnidia of *Gymnosporangium globosum* on upper surface of leaf of *Crataegus mollis*.

GYMNOSPORANGIUM NELSONI ARTH.

On *Juniperus scopulorum* Sarg. (Shenandoah, 1929). Galls of this rust were found on nursery trees which had been brought from Colorado in March, 1929. It is not probable that *G. nelsoni* is native in Iowa.

SEASONAL DEVELOPMENT OF *GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE* AND *G. GLOBOSUM* IN IOWA

Extensive investigations on seasonal development were reported 15 years ago by Reed and Crabill (44) in Virginia, Giddings and Berg (27) in West Virginia, Jones and Bartholomew (34) in Wisconsin, and Weimer (56) in New York, while but little work on cedar-apple rust has been done in Iowa.

Seven species of *Gymnosporangium* have been shown to exist in the state, of which only cedar-apple rust (*G. juniperi-virginianae*) and hawthorn rust (*G. globosum*) occur commonly. In this section attention will be confined to these two common rusts with emphasis on their destructiveness and on phases of their seasonal development.

GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE

Cedar-apple rust was not recorded as a disease of economic importance in Iowa before 1900. Pammel (39) reported the

fungus to be so abundant in 1905 as to seriously impair the vitality of the red cedar, *Juniperus virginiana* L., of adjacent trees of wild crab, *Pyrus ioensis* (Wood) Bailey, and of the cultivated apple, *Pyrus malus* L. The epidemic of 1928 was considered by experienced nurserymen and orchardists to be the most serious outbreak of the



Fig. 4. Galls of *Gymnosporangium globosum* on twigs of red cedar showing teleutosori before wetting.

disease in many years. The years 1918, 1923 and 1925, are also recorded as periods of serious infestations.

Losses incurred by nurserymen were attributed mostly to the devitalizing effect of the disease on young trees. In 1928, al-

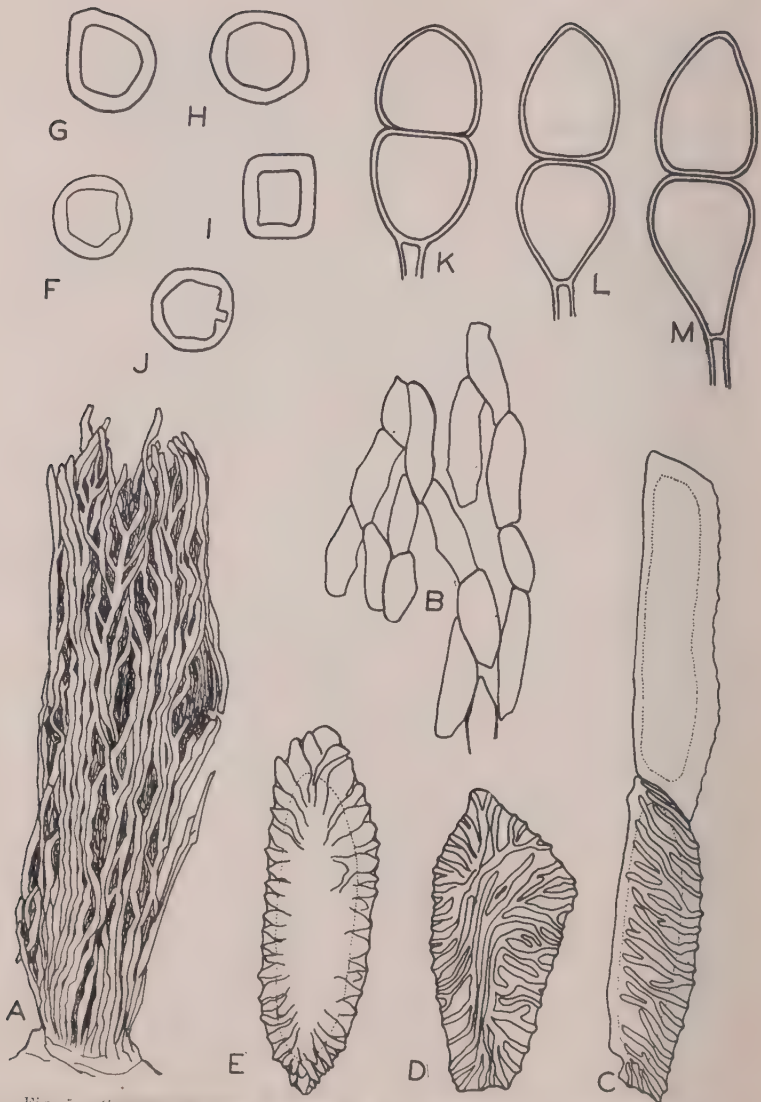


Fig. 5. *Gymnosporangium globosum*. A. An accidium. The peridial cells have split apart allowing the escape of the accidiospores. X63. B. A group of peridial cells in face view. These cells seem to be attached more securely at the ends than at the sides. X215. C. Two peridial cells in side view. Ridge-like papillae cover the inner and side walls. X652. D. Inner face view of a peridial cell. X652. E. A peridial cell in outer face view. X652. F-J. Accidiospores. X652. K-M. Teliospores. X652.

most complete defoliation and serious cankering of stems in Bechtel's double-flowering crab caused the loss of about 2,500 trees valued at \$1,500 in one nursery at Shenandoah. Susceptible varieties of apples in nursery rows also suffered, but to a less degree, from loss of leaves and branches weakened by rust cankers. During 1928, however, cedar-apple rust was by far the most destructive disease found on leaves and stems of young apple trees at Shenandoah. The stunting of ornamental red cedars due to gall formation was not measured but was estimated to be appreciable in some cases.

Apple orchards were affected by cedar-apple rust through the partial defoliation of trees and blemishes on the fruit. The loss of leaves resulted in general devitalization of trees accompanied by weak growth and low yields of fruit, while the fruit blemishes affected the quality of the crop of the current year. Rust was found on 11 to 22 percent of the fruit in three representative orchards of Jonathan in Raglan Township, Harrison County, on Aug. 27, 1930. The destruction of leaf area in the same orchards ranged from 1.72 to 3.84 percent.

The most damaging results from cedar-apple rust were observed in a home orchard south of Shenandoah where trees of Jonathan apple interlocked branches with red cedar trees, a condition which had existed for about 10 years; both the red cedar hedge and the apple orchard were very seriously damaged.

SPORULATION OF GALLS

A uniform lot of air-dried galls of *G. juniperi-virginianae* was taken May 20, 1929, from the same tree and immersed in tap water at 14.5°C. for different periods up to 180 minutes. Following immersion, the galls were suspended in air at 18 to 21°C. and examined microscopically at various times during the following 24 hours. As indicated in table I, abundant sporulation developed in 4 to 5.3 hours after removing the galls from water. Promycelia and sporidia grew more rapidly from sori soaked 2 to 3 hours than from those immersed for only 30 minutes. The time required to produce abundant sporulation from air-dry galls, however, was from 6 to 7 hours regardless of whether the period of soaking was 30 or 180 minutes. There seemed to be

TABLE I. TIME REQUIRED FOR SPORULATION OF GALLS OF *G. JUNIPERI-VIRGINIANAE* AS INFLUENCED BY VARIOUS PERIODS OF SOAKING AND DRYING.

Gall no.	Immersed (minutes)	Dried (minutes)	Time required for sporulation (minutes)
1	None		No sporulation
2	..		..
3	30	320	350
7	90	317	407
10	120	220	340
14	180	235	415

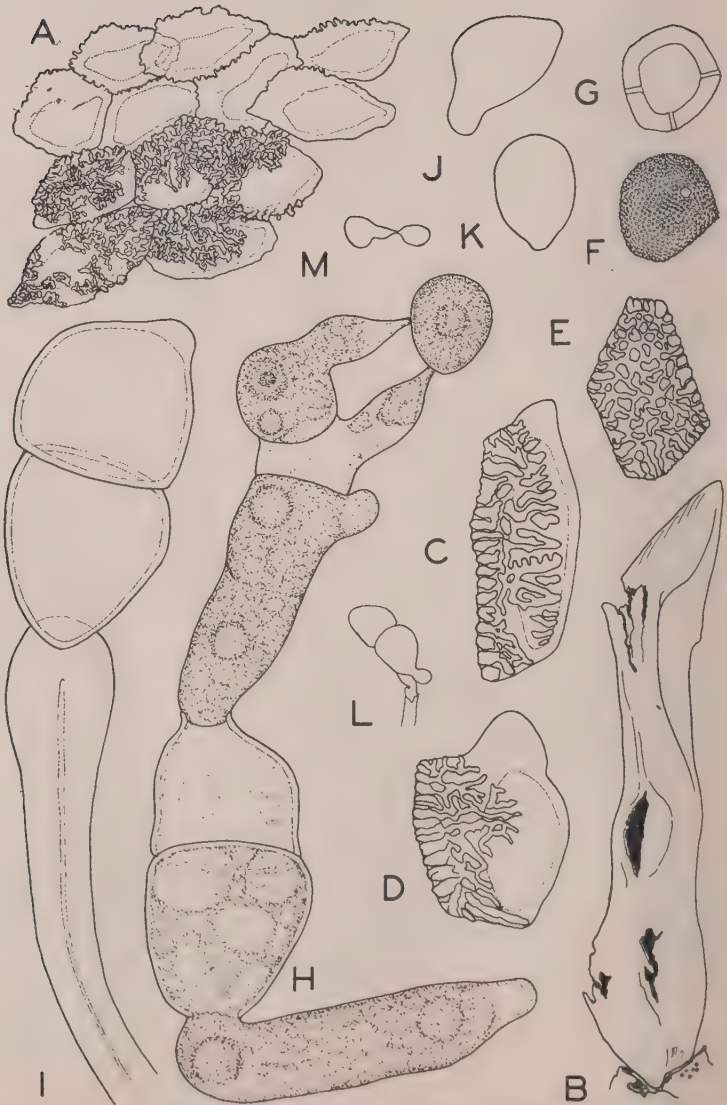


Fig. 6. *Gyano sporangium germinale*. A. A group of peridial cells. X250. B. An accidium. X24. C-D. Peridial cells in side view. X497. E. A peridial cell as seen from the inner face. X197. F-G. Accidiospores; fig. 6f illustrates the coarsely verrucose papillae on the surface; fig. 6g, an optical section through three germ pores. X504. H. A germinating teliospore. X878. I. A teliospore and its typically carotiform pedicel. X878. J-K. Sporidia. The spore in fig. 6j has begun to germinate. X878. L. A sketch of a germinating teliospore showing how the pedicel is broken by the promycelium of the lower cell. M. A sketch showing the formation of a secondary sporidium.

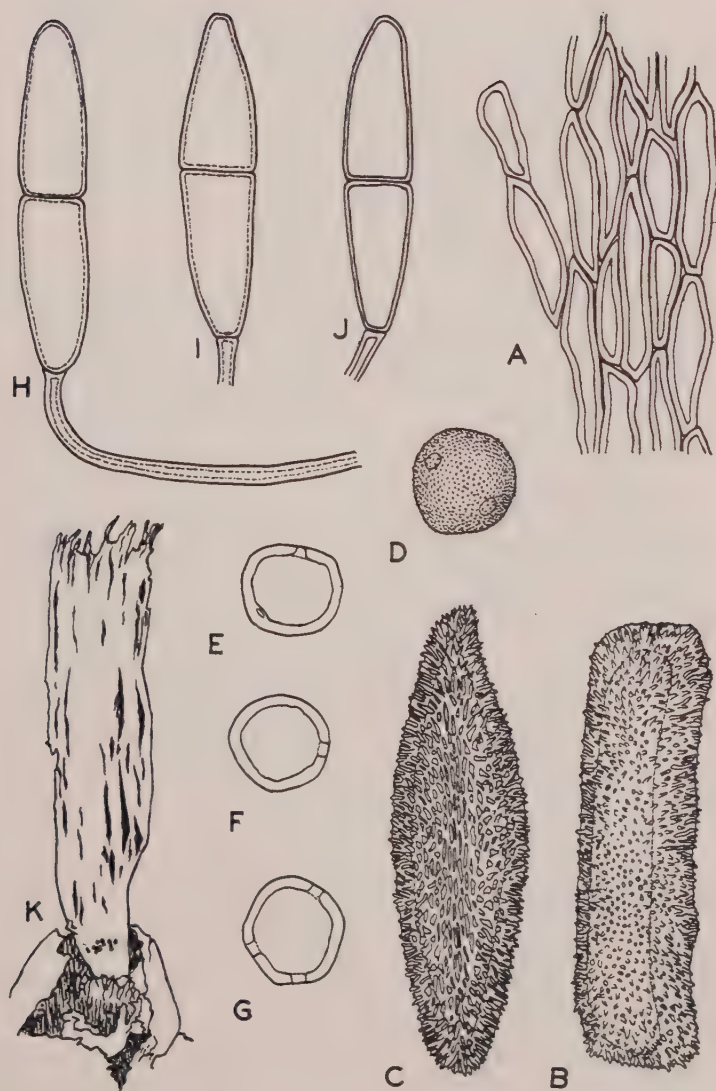


Fig. 7. *Gymnosporangium clavariaeforme*. A. A group of periodical cells. X220. B. A peridial cell in side view. X627. C. The inner face view of a peridial cell X627. D-G. Accidiospores. Fig. 7d shows surface markings while figs. 7e-g illustrate optical sections through germ pores. X627. H-J. Teleutospores. X700. K. An acidium, the top portion of which has been shattered. Some accidiospores are shown near the base. X24.

no difference in the condition of teleutospores whether they were soaked for 24 hours or for 1 hour. In both cases swellings appeared at the germ pores, but germination proceeded no farther until air was supplied. The rate of growth from that time was about the same.

Fully-expanded sori placed on the surface of 3 percent plain agar in a closed petri dish sporulated as freely as those attached to the gall. Discharged sporidia were found on the agar at a distance of 713 μ from the edge of the sorus.

GERMINATION OF TELEUTOSPORES

Germ tubes coming from teleutospores remained non-septate when held in a film of moisture. Normal septation occurred only when the tubes projected away from the water and into the air. Although swellings appeared at all of the two or three germ pores in each cell of teleutospores soaked for 60 minutes, only one germinal tube developed. The two cells of the teleutospore seem to act independently when germinating. Conditions causing the development of one may not affect the other at the same time, thus tending to prolong the period of sporulation.

The formation and discharge of sporidia were similar to these processes in *Puccinia graminis* Pers. as described by Buller (13). Steps in teleutospore germination are illustrated in fig. 8. After the sterigma is formed, the migration of the protoplast from the promycelial cell to the sporidium requires 20 to 30 minutes. After a short period of quiescence, a small drop of liquid appears at the point where the sporidium is attached. While the drop increases rapidly in size, the sporidium seems to shrink. The spore is soon jerked to one side and discharged into the air. In two instances the interval between the first appearance of the drop and the discharge of the spore was 10 and 13 seconds, respectively. The tenacity with which sporidia adhered to dry objects placed below sporulating galls, indicates that these spores are very sticky.

AECIDIOSPORE GERMINATION

Fukushi (24) showed that exposure to low temperatures increased the germinability of aecidiospores of *Gymnosporangium yamadac* Miyabe. Thomas and Mills (54) obtained similar results with aecidiospores of *G. juniperi-virginianae* and *G. globosum*. Miller (36), working with cedar-apple rust, found that aecidiospores held under natural conditions germinated most readily between January and April. Because these investigators experienced difficulty in germinating aecidiospores during the summer, they infer that red cedars are not infected before late fall or early spring.

Many attempts were made to germinate aecidiospores of *Gymnosporangium juniperi-virginianae*. Diseased leaves of *Pyrus malus* L. and *P. ioensis* var. *plena* Rehd. were collected at vari-

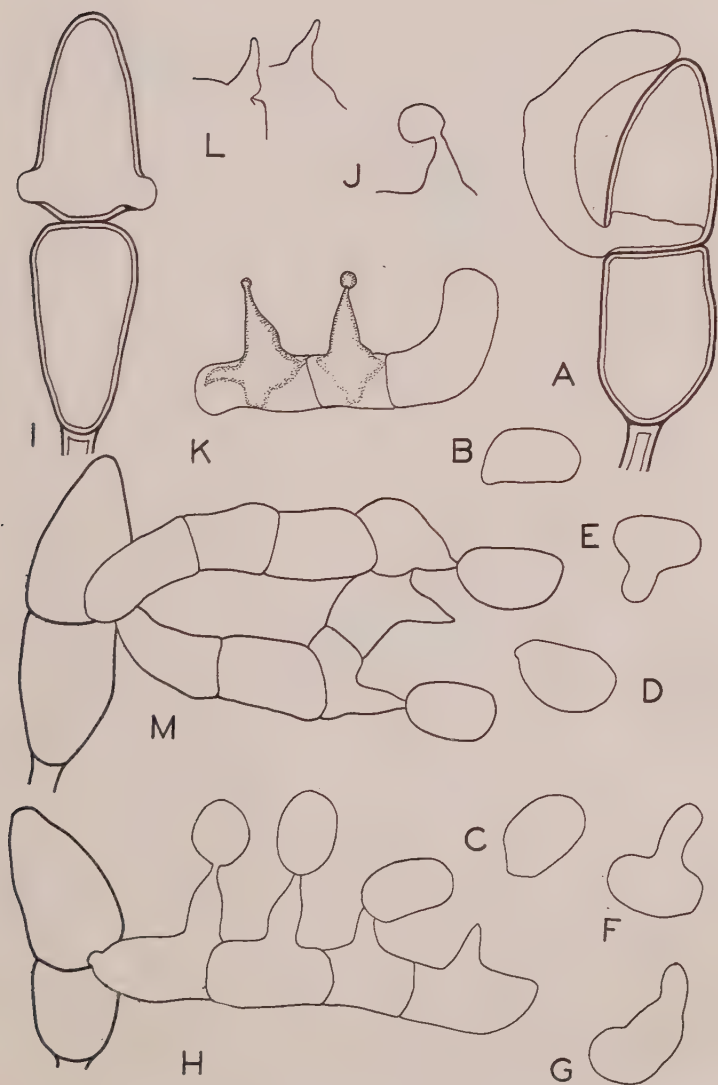


Fig. 8. *Gymnosporangium juniperi-virginianae*. (All figures magnified 850 diameters.) A. A teliospore with a germinal tube at the stage previous to septation. B-D. Sporidia. E-G. Germinating sporidia. H. A teliospore with a promycelium and three sporidia. The distal cell is empty. I. A teliospore with swollen germ pores. J-L. Sterigmata arising from promycelia and showing stages in the development of sporidia. M. A teliospore with two sporulating promycelia.

ous times between Aug. 22 and Nov. 4, 1929, and were held in cloth sacks out-of-doors until used. Not more than 2 percent germination was obtained in any case, and many attempts failed completely. Aecidiospores from fresh apple leaves collected on Oct. 28, and incubated for 18 hours at room temperature on the surface of a hanging-drop of water, showed 2 percent germination. The spores observed in these trials were usually much shrivelled and remained in that condition even after resting on water for several hours.

Newly-matured aecidiospores were collected in 1930 by shaking infected leaves of *Pyrus ioensis* var. *plena* over a sheet of paper. The spores were placed in closed glass vials and held either in the laboratory at room temperatures of 20 to 41°C. or in a refrigerator at 5 to 13°C. Tests were made soon after collection and at subsequent times until germination ceased. The spores were dusted on a drop of distilled water on a cover slip which was inverted over a Van Tieghem cell. Counts of 300 to 1200 spores each were made after an incubation of 20 to 52 hours at room temperatures. One lot of aecidiospores collected July 28, gave 54 percent germination when tested immediately. Figure 9 depicts the effect of refrigeration on another sample of aecidiospores obtained on July 31. These spores showed 16.8 percent germination when collected; but after the lot was divided, the percentage of germination in the refrigerated portion increased rapidly for at least 22 days, while that held at room temperature for the same interval dropped to zero. From Aug. 21 to Oct. 7, the proportion of viable spores held at low temperatures decreased from 57 to 1.1 percent, and by Nov. 24 no germination

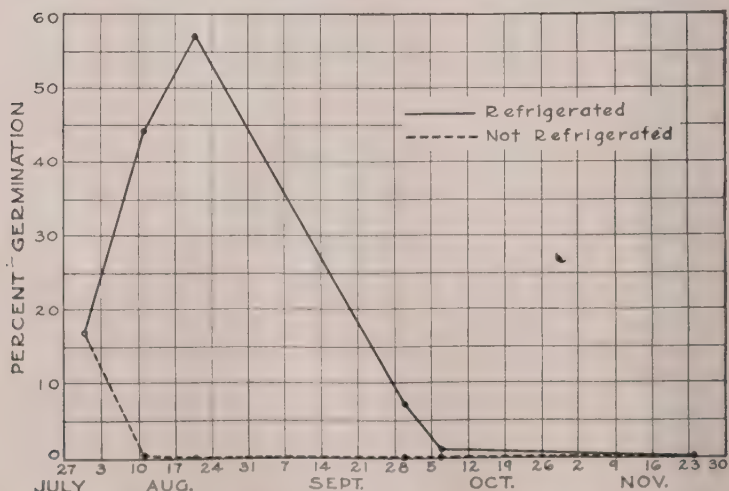


Fig. 9. Graph showing effect of refrigeration at 5 to 13°C. on the germination of aecidiospores of *G. juniperi-virginianae* collected July 31, 1930.

was detected. A similar response was obtained from another lot of aecidiospores collected Aug. 6. After 31 days the refrigerated portion contained 20 times as many viable spores as did the portion held in the laboratory.

These results confirm the work of Fukushi (24), Thomas and Mills (54) and Miller (36) regarding increased germinability as the result of exposure to low temperatures, but the indication that newly-matured aecidiospores may germinate to the extent of 54 percent in July suggests a different interpretation. It is possible that desiccation may affect the power of germination since spores exposed to high summer temperatures became shriveled and lost vitality more rapidly than others kept in the refrigerator. As will be shown in table IV (page 356), red cedars were successfully inoculated in August and September. Most of the aecidiospores used in these inoculations were collected on Aug. 6 and were placed on the junipers immediately or after refrigeration at 5 to 13°C. These results suggest that aecidiospores of *G. juniperi-virginianae* may infect the red cedar when liberated from the aecidium but that refrigeration will prolong and increase their germinability.

TIME OF DEVELOPMENT OF THE DIFFERENT STAGES

At Shenandoah, near the southwestern corner of Iowa, the growing season often begins a week earlier than at Ames and about 2 weeks earlier than at the northern boundary of the state. These differences are reflected in the development of cedar-apple rust, sporulation of galls occurring earlier in the south than in the north. The dates given in table II regarding the seasonal development of the fungus at Shenandoah, 1927-1930, do not, therefore, apply to all portions of Iowa.

TABLE II. OBSERVATIONS ON THE SEASONAL DEVELOPMENT OF *G. JUNIPERI-VIRGINIANAE* AT SHENANDOAH, IOWA, 1927-1930.

Year	First sporulation sori	Period maximum sporulation	Number sporulations	First open aecidia	First appearance new galls
1927				July 21	
1928		May 14-18		" 18	
1929	April 19	" 10-13	5	" 18	July 2
1930	" 17	" 1	8	" 5	June 18

In 1929, viable teleutospores were last collected in the open on July 10, 82 days after the first sporulation. Functional aecidia were found on *Pyrus ioensis* var. *plena* 56 days after the pycnidia appeared. Artificial inoculations had shown the period of incubation to be about 16 days on this host. It may be assumed, therefore, that about 72 days elapsed between infection and first opening of the aecidia. Very small galls, 1 mm. in diameter, were discovered on red cedar trees on July 2. In order to prove more definitely that new galls were just appearing, six branches of *Juniperus virginiana* were selected at random and all visible galls were removed. Eighteen days later, at least one tiny gall was found on each of five branches. No aecidia could

be found on nearby apple trees so it seemed that acediospores of 1929 could not have brought about the new galls. Furthermore, these galls were not on wood of the current season, but on that of the previous year.

Galls of the cedar-apple rust are usually functional one year only. New tissue, however, is sometimes proliferated at the side of or partly surrounding old galls and teleutosori develop from this in the following year. In one instance it was estimated that 20 percent of the galls had produced their second crop of spore horns, while one gall seemed to bear the scars of sori of three successive years.

EFFECT OF DROUTH AND HIGH TEMPERATURES

The number of viable galls was very great in 1930, and conditions during May and June were favorable to widespread infection on apples. Drouth and exceedingly high temperatures developed in southwestern Iowa following July 4, and continued until September. The abnormal conditions did not seem to interfere with the full development of rust on apples, but very few of the new galls on the red cedars lived until fall. In the cedar-apple rust nursery at Ames, trees that had borne many new galls in 1929, were nearly free from new galls in September, 1930.

INFECTION TRIALS ON THE RED CEDAR

A number of experiments were conducted to induce artificial infection of the red cedar and to study the length of time between infection and the maturity of teleutospores. Two 3-year-old plants of *Juniperus virginiana* were potted on May 28, 1929, and set in the ground near six trees of Beechtel's flowering crab that were infected severely with *G. juniperi-virginianae*. On July 22, at the time when acedidia of cedar-apple rust were just beginning to open, a sack of glass cloth was tied over one of the trees to shield it from infection and was not removed until Sept. 25. The second tree was not protected. Many tiny galls were discovered on the unprotected tree on June 18, 1930, while there were none on the control. The galls were emerging from leaves which had formed in 1929. They increased in size during the remainder of that season and formed mature spores in the spring of 1931.

Red cedar trees, 15 to 20 inches tall, were transplanted in wooden nail kegs, in groups of 10 to 15 each. The trees were taken into the greenhouse on July 26, 1929, 8 days after the first open acedidia had been found. A few cedar rust galls were developing on the plants at the time, but these were removed. Table III describes the inoculations and gives readings on the total number of galls found on these trees during 1930. Observations on the control plants indicate that some natural infection occurred. Only in the case of pots No. 503 and 504 is there good evidence that additional infections occurred because

TABLE III. INOCULATIONS OF RED CEDARS WITH AECIDIOSPORES OF *G. JUNIPERI-VIRGINIANAE* IN 1929.

Pot. no.	Dates of inoculation 1929	Method of inoculation	Total no. galls found			
			April 24, 1930	June 18, 1930	July 5, 1930	Aug. 25, 1930
500	Aug. 10 to Aug. 17	Diseased branches of <i>Pyrus ioensis</i> placed over plants in greenhouse. Water applied daily by sprinkling.				
503	Aug. 20 to Aug. 30	Pot placed below infected trees of <i>Pyrus ioensis</i> out-doors.	0	0	3	5
504	"	"	0	20	64	65
505	Aug. 22 to Aug. 30	Pot placed below infected trees of Jonathan apple in orchard of George Bird.	0	5	31	34
506	"	"	0	3	2	2
514	Sept. 3 to Sept. 5	Freshly picked, infected leaves of <i>Pyrus ioensis</i> placed on plants in greenhouse. Plants covered by moist empty nail keg.	0	0	0	2
518	Sept. 3 to Sept. 6	As above. But infected leaves allowed to remain on plants for 24 hours longer without covering to retain moisture.	0	0	11	11
525	"	Pot placed below diseased tree of <i>Pyrus ioensis</i> in the open.	0	0	0	5
501	—	None	0	0	0	2
502	—	None	0	0	0	1
512	—	None	0	0	1	3
513	—	None	0	0	0	5
517	—	None	0	0	0	1
519	—	None	0	0	0	0
520	—	None	0	0	3	5
521	—	None	0	0	2	3

of the inoculation. The galls produced in this experiment were forming spore horns when observed April 8, 1931.

More extensive inoculation experiments were made during August and September, 1930, on 3-year-old seedlings of *Juniperus virginiana* in pots. These trees were of a uniform lot, thrifty in appearance and standing about 1 foot in height. The aecidiospores were collected for the most part on Aug. 6, 1930, and all were from *Pyrus ioensis* var. *plena*. They were stored in closed glass vials at 5 to 13°C. until used and a portion of them was known to be viable throughout the period. Methods used in inoculation together with results obtained are given in table IV. Wounding consisted merely of clipping off the tips of branches with scissors. A Devilbis atomizer was used for spraying the water and spore suspensions. Spores were dusted on the plants by blowing them from a paper. Following inoculation, the plants were placed in a chamber lined with wet sphagnum moss for a period of 36 hours and then were returned to a partially shaded cold frame out-of-doors.

A notable feature of these experiments was the wide variation in number of galls found on trees which had received similar treatments. Uniform inoculation and treatment of five red cedars resulted in the development of 3, 72, 22, 7 and 0 galls,

TABLE IV. ARTIFICIAL INOCULATION EXPERIMENTS USING AECIDIOSPORES OF *G. JUNIPERI-VIRGINIANAE* FROM *PYRUS IOENSIS* VAR. *PLENA* ON POTTED RED CEDAR TREES. (August 9 to Sept. 10, 1930).

Treatment of trees	Total no. galls 6-26-31	No. trees	Av. no. galls per tree	Ratio
Inoculated	343	33	10.4	83.2:1
Not inoculated (control)	2	16	0.125	
Wounded, inoculated	122	13	9.4	1:1.18
Not wounded, inoculated	221	20	11.05	
Inoculated, sprayed with water	253	29	8.72	1:2.58
Inoculated, not sprayed with water	90	4	22.5	
Dusted with aecidiospores	325	27	12.04	4.01:1
Sprayed with suspension of aecidiospores in water	18	6	3	
Sprayed with water before dusting with aecidiospores	83	13	6.39	1:2.38
Sprayed with water after dusting with aecidiospores	152	10	15.2	

respectively. This variability may have been due to error; it is also possible that different red cedar seedlings vary in disease resistance.

In these experiments, undoubtedly infection was secured by artificial means. The data indicate further that dusting is a more successful method of inoculation than spraying with a spore suspension. It seems better to spray the plants with water after dusting than before, but no spraying is necessary if a period of high humidity follows inoculation. Evidently, wounding is not a factor except that it may lessen the amount of infection by reducing the susceptible leaf area.

GYMNOSPORANGIUM GLOBOSUM

Both the apple and hawthorn rusts are found on *Juniperus virginiana* L. and *J. scopulorum* Sarg., but in Iowa no pomaceous plant is known to be a common aecidial host. Since the hawthorn rust is comparatively rare on the pear, *Pyrus communis* L., and its other hosts (*Crataegus* spp. and *Juniperus* spp.), which are chiefly of ornamental value, it does not seem to be of great economic importance in the state. The study of its seasonal development, life cycle and host response is not without value, however, because this rust has recently been reported on the cultivated apple, *Pyrus malus* L., in New York by Thomas and Mills (54) and in Indiana by Miller (36) where considerable damage is done.

At Shenandoah, the aecidia of *G. globosum* were found to mature from 27 to 41 days later in summer than those of *G. juniperi-virginianae*. From table V it will be seen that the appearance

TABLE V. OBSERVATIONS ON THE SEASONAL DEVELOPMENT OF *G. GLOBOSUM* AT SHENANDOAH, IOWA, 1927-1931.

Year	First sporulation sori	Period maximum sporulation	First open aecidia	First appearance new galls
1927			Aug. 17	
1928			" 23	
1929	April 20?	May 10-13		Oct. 25
1930	" 25	April 25-May 1	" 15	Sept. 20

of new galls on red cedars was noted in late September and October, three months after galls of cedar-apple rust had become visible. If *G. globosum* is biennial in its life history as shown by Dodge (22), proof for such a contention cannot rest on the comparative dates on which new galls appear and on which aecidia open.

In Iowa most of the infection from sporidia occurs at one period sometime during May. Teleutosori do not possess the power of repeated sporulations, as in the apple rust, but when fully expanded, they seem incapable of drying down to their previous size or shape. Instead, the masses of jelly coalesce and individual sori lose their identity. Sporidia are discharged for a period of 2 or 3 days while the jelly is drying and then the yellow mass becomes hard and amorphous. Galls with expanded spore horns are shown in fig. 10a. Individual sori from galls 3 mm. in diameter may reach dimensions of 10-20 by 5-12 mm. at maximum expansion.

The period between infection by sporidia and the opening of aecidial cups seems to be somewhat longer than that for cedar-apple rust. In one case recorded, pycnidia appeared on leaves of *Crataegus mollis* after 23 days and open rosettelia were found 81 days after artificial inoculation. Aecidia developed abundantly on leaf veins, petioles, fruit and succulent branches. Stem cankers were most common at the nodes, but systemic infection of dormant buds did not occur.

The mycelium of *G. globosum* often becomes perennial in the red cedar, but in the smallest galls it usually dies after its first season of sporulation. In junipers where this rust was very abundant, more than half of the new galls died each year during 1929 and 1930. Death was probably due to a lack of food.



Fig. 10. *Gymnosporangium globosum* on red cedar. A. Expanded teliosori showing their typical wedge shape. B. Leaves of red cedar showing early symptoms of hawthorn rust. Gall tissue is protruding slightly through the torn epidermis in the right hand leaf.

More intensive study of gall development was made on a naturally infected tree of red cedar transplanted into the greenhouse on Oct. 25, 1929. Almost without exception, the new galls which had appeared by Oct., 1929, produced one or more sori by Feb., 1930. A considerable number of leaves, however, did not show infection until January. Chlorotic areas, often banding the leaves, marked the diseased tissue. The affected parts soon became swollen and cracked longitudinally along the inner (upper) surface. Sections through the chlorotic zones of leaves shown in fig. 10 b, revealed abundant intercellular mycelium in the parenchyma tissue. About the vascular bundle some browning of the cells was evident. Comparison with sections through the green portion of the same leaves showed fewer chloroplasts in diseased than in healthy cells. In the latter the chloroplasts were very numerous and were spaced evenly about the cell walls. No rust mycelium was found outside of the chlorotic zone. In other leaves where hypertrophy had progressed further, the cells were packed together solidly—a condition very unlike that in normal leaves where spongy parenchyma surrounds the vascular cylinder. The leaf is usually ruptured along the upper surface. All of the stomata are situated here, and this surface is not strengthened by underlying sclerenchyma cells as is the case in the other surfaces.

Steps in the development of galls of *G. globosum* on the red cedar are illustrated in fig. 11. In fig. 11 a, a chlorotic zone is situated in the middle of the leaf blade while in fig. 11 b, the infected tissue extends from the leaf blade downward along the sheath. Cracks have appeared in the epidermis of both leaves indicating internal hypertrophy. Portions of the leaves not invaded by the rust have retained their normal shape and color. Later stages in the growth of gall tissue are shown in the other figures. The epidermis is split and broken as the gall enlarges. Often the tip of the needle is killed, but the needle remains attached to the gall. Figure 11 e illustrates the manner in which a gall may bend the terminal bud abruptly to one side. A small excrecence with a sorus is shown in fig. 11 f, arising from a chlorotic and much swollen leaf blade.

These observations indicate that the disease is localized on the red cedar and may be found at any point along the leaf blade or extending downward on the sheath. In a few cases the lesion seemed confined entirely to the sheath. In young stems the leaf sheaths completely enclose the vascular cylinder, the true bark developing only after a period of 2 years at which time the leaves are shed. Galls arising from tissue in the leaf sheath usually attain greater size than those situated on the blade. The former may completely surround the stem after several years and give the impression that infection originated within it. The evidence, however, supports the conclusion reached by Weimer (57) that galls of this species originate in the leaves.



Fig. 11. Galls of *Gymnosporangium globosum* on red cedar. (All figures magnified 5.26 diameters.) A. Early symptoms of infection. A short, longitudinal crack has formed opposite a slight swelling in the chlorotic zone of the diseased leaf. B. The infected portion of this leaf is chlorotic and extends from the blade downward on the sheath. C. Gall tissue has lifted the infected needle away from the stem. A strip of epidermis is still attached from the back of the needle to the base of its sheath. D. Two galls arising from one needle. Teleutospores have appeared on each swelling. E. A gall with a mature teleutosorus which has grown from the sheath of the infected leaf and has turned the terminal bud of the twig sharply to the side. F. A tiny globose gall bearing teleutospores developed from a much swollen leaf.

Dodge (22) obtained mature teleutospores of *G. globosum* about 21 months after sowing aecidiospores on red cedars. Weimer (56) found new galls of this rust on July 25, 1914, before any aecidia were open. The galls sporulated the following spring, indicating that 2 years were required to complete the life cycle. In the present study, new galls of *G. globosum* have not been detected in nature before the maturity of aecidiospores, but there is no evidence to contradict the conclusions of Dodge and Weimer regarding the length of the life cycle. Although first symptoms of gall formation appeared in January, 1930, on leaves which were developed presumably in 1929, these galls did not produce sori during that year. Their appearance may be explained by the fact that the dormancy of the tree was broken prematurely by transplanting in the greenhouse.

Aecidiospores of *G. globosum* were obtained from fallen leaves of hawthorn in Nov., 1929. In 26 trials, the percentage of germination varied from zero to 90. The largest percentage was obtained in a drop of water containing two leaves of red cedar. The viability of spores held at 5°C. for 6 weeks did not seem to increase, nor did that of others kept in the open. Germination was obtained at several temperatures of incubation from 19.7 to 32°C.

In 1930, composite collections of aecidiospores were obtained in August and September from newly-opened roestelia on leaves of *Crataegus* spp. Methods similar to those used with *Gymnosporangium juniperi-virginianae* were employed to test viability, but spores refrigerated at 5 to 13°C. over periods of 1 week to 3 months did not germinate. One lot collected on Oct. 14 and held at 5°C. for 41 days gave 31.2 percent germination; but only a trace of germination was obtained from similar spores at time of collection, and others of the same lot seemed to be non-viable after 89 days of refrigeration. The spores collected on Oct. 14 were not threshed from leaves until they were needed. For this reason, the samples may not have been so uniform as those of the earlier composite collections.

The only appreciable germination of aecidiospores of *G. globosum* reported by Weimer (56) was obtained from material exposed outdoors until Nov. 8. Thomas and Mills (54) found 54 percent germination in a single mount of aecidiospores collected on Dec. 12 from fallen leaves of *Crataegus*.

STUDIES ON PATHOGENICITY

Adequate information regarding seasonal development of the cedar rusts can be obtained only where these fungi reach full maturity on their respective hosts. In this chapter it will be seen that the cedar-apple and hawthorn rusts, as they occur in Iowa, can reach full maturity only on a relatively small number of the available pomaceous and coniferous plants.

PATHOGENICITY OF *GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE*

Thaxter (53) observed, more than 40 years ago, that cedar-apple rust does not develop to the same extent on all of its hosts. Fulton (25) observed that leaves of "susceptible" varieties of apples are resistant to infection when first emerging from the bud and again when fully grown and matured. Giddings and Berg (27) attribute the immunity of old leaves to the thickness of the cuticle and cell walls and also to other unnamed chemical and physical changes inside the leaf. In considering the nature of disease resistance, Reed and Crabill (44) discerned two types: (1) The parasite fails to penetrate the epidermis because of mechanical or morphological barriers, although when once inside the palisade and mesophyll tissues, it finds a congenial environment; (2) The parasite enters the leaf as in the case of a susceptible host, but its development ceases before normal fruiting structures are produced. The first type of resistance was demonstrated by Miller (36) who obtained infection "through wounds on apple leaves which had become resistant."

The relative susceptibility of apple varieties to cedar-apple rust has been reported by Chester (14), Stone (50), Giddings and Berg (27), Jones and Bartholomew (34) and many others. While space does not permit the publication of a full compilation of these observations, the wide variation in reports on the susceptibility of certain varieties can be judged by four cases cited in table VI. The readings are listed by states for the purpose of stressing geographical relationships.

In Iowa before 1905, when Pammel (39) reported a general outbreak of cedar-apple rust, the apparent resistance of apples to this disease was a matter of considerable speculation. Halsted (29) first called attention to the resistance of apples to cedar-apple rust in Iowa, while at the same time apples in the eastern states were much affected by the disease. Stewart and Carver (49) undertook to explain this difference and concluded that the apples grown in Iowa were resistant to rust. Arthur (6) compared strains of cedar-apple rust from North Carolina and Iowa, but found no difference between eastern and western forms in the ability to infect the cultivated apple. Weimer (56) reached the same conclusion regarding the strains of rust from Nebraska, Virginia and New York and suggested that apples in certain sections may vary in relative susceptibility.

Orton and Wood (37) suggested that the apparent discrepancies in reports from various states concerning the susceptibility of varieties of apples may be due in part to the presence of different biological races of cedar rust which react differently to the same variety of host. They attribute a similar theory to Waite (55). Bliss (12) made a preliminary statement on experiments which suggest the existence of biologic specialization in *G. juniperi-virginianae*.

TABLE VI. A COMPILATION OF REPORTS FROM VARIOUS STATES ON THE RELATIVE SUSCEPTIBILITY OF FOUR VARIETIES OF CULTIVATED APPLE TO *GYMNOSPORANGIUM JUNPERI-VIRGINIANAE*.*

Variety	Immune	Very resistant	Resistant	Susceptible	Very susceptible
Ben Davis		Ky. e	Ia. 1 Neb. 1 N. Y. 2 N. C. 1	Ark. b Del. 1 Ill. 1 Mo. 1 N. C. b O. b; O. 1 Penn. b Tenn. b Va. 2; Va. 3 W. Va. 1; W. Va. 2	Ark. g Ia. a N. Y. 3 Tenn. c Va. 1
Grimes	Va. 2	Mo. 1 Va. 1 W. Va. j.	Ill. 1 Kan. i Ky. e Neb. 1 W. Va. 1 W. Va. 2	Ala. 1 Ind. k Neb. 1 N. J. j S. C. b Va. 3	Del. 1
Oldenberg		Ky. e Minn. j Mo. 1	Ia. 2 Ill. 1 Minn. b Neb. 1 N. Y. 3 N. C. 1	Conn. 1 Ind. k Va. b	Va. j
York Imperial		Kan. i	Ky. e Neb. 1 N. C. 1	Ala. 1 Ill. d Ind. d Md. c N. Y. a Penn. b W. Va. 1	Del. 1 Ill. 1 Md. g Penn. a Va. 1; Va. 2; Va. a Va. 3 W. Va. 2

* Footnotes for table VI with interpretation of authors' descriptions of susceptibility.

Ala. 1 = Stone (50)

Very resistant = "free from rust"

Susceptible = "slightly affected"

Very susceptible = "badly affected"

Conn. 1 = Clinton and McCormick (15)

Very resistant = "failed"

Resistant = "poor take"

Susceptible = "successful"

Del. 1 = Chester (14)

Resistant = "free from rust"

Susceptible = "slightly affected"

Very susceptible = "badly affected"

Ia. 1 = Stewart and Carver (49)

Ia. 2 = Pammel (39)

Ill. 1 = Anderson (2)

Very susceptible = "most susceptible"

Susceptible = "moderately"

Resistant = "resistant"

Mo. 1 = Talbert (51)

Neb. 1 = Emerson (23)

N. Y. 2 = Stewart and Carver (49)

N. Y. 3 = Stewart (48)

Very resistant = "resistant"

Resistant = "nearly or quite free"

Susceptible = "slightly affected"

Very susceptible = "very susceptible"

N. C. 1 = Smith and Stevens (46)

Resistant = "Especially resistant"

Susceptible = "susceptible"

O. 1 = Selby (45)

Resistant = "not susceptible"

Susceptible = "moderately susceptible;" "somewhat susceptible"

Very susceptible = "foliage susceptible;" "very susceptible"

- Va. 1 = Reed and Crabill (44)
 Very resistant = "practically immune"
 Very susceptible = "very susceptible"
- Va. 2 = Reed, Cooley and Crabill (43)
 Immune = "distinctly resistant or even immune"
 Susceptible = "moderately susceptible"
 Very susceptible = "most susceptible"
- Va. 3 = Reed, Cooley and Rogers (42)
 Resistant = "more or less resistant"
 Susceptible = "moderately susceptible"
 Very susceptible = "most susceptible"
- W. Va. 1 = Giddings (26)
 Immune = "immune"
 Resistant = "resistant"
 Susceptible = "moderately susceptible"
 Very susceptible = "susceptible"
- W. Va. 2 = Giddings and Berg (27)
 Immune = "immune"
 Resistant = "resistant"
 Susceptible = "moderately susceptible"
 Very susceptible = "susceptible"
- a = Hesler and Haskell (32) g = Giddings and Wood (28)
 b = Hutchins and Haskell (33) i = Archer (4)
 c = Anderson (3) j = Bennett (9)
 d = Haskell and Wood (31) k = Haskell (30)
 e = Adams (1)

Thomas and Mills (54) reported that in the Hudson River Valley during 1927 and 1928, not only *G. juniperi-virginianae*, but *G. globosum* and *G. germinale* caused destructive diseases on apples. Miller (36) successfully inoculated varieties of apples with the same three species of rust in Indiana. Bliss (11), however, was unable to produce infection artificially on apples with *G. globosum* in Iowa and did not find it occurring naturally on 150 varieties of apples and ornamental crabs in the field.

METHOD OF MEASURING RELATIVE SUSCEPTIBILITY

The terms which have been used heretofore in denoting the relative susceptibility of apples to cedar-apple rust have lacked uniformity and have often been poorly defined. After allowing for discrepancies which may have come about because of this confusion, the reports concerning the disease on certain varieties indicate wide differences in the virulence of rust in various localities. Although several workers had failed to demonstrate these differences experimentally, considerable circumstantial evidence remained to indicate their reality. In the present investigation it seemed desirable to further investigate this question and, as a preliminary step, devise a method for measuring relative susceptibility.

If the development of a rust lesion on a leaf of Wealthy apple is followed chronologically, three steps in the maturity of the parasite may be observed: first, chlorotic flecks appear where infection from sporidia has occurred; second, pycnidia develop in lesions on the upper surface; and third, acedial cups break through the swollen tissues of the lesion on the lower surface. If the development of the fungus is followed on Yellow Transparent, it will be found that pycnidia arise from flecks, but no acedial are formed. The degree of maturity reached by the rust on this variety ends with pycnidial formation. Likewise, cedar-apple rust produces only flecks on Northwestern Greening and it leaves

no visible symptoms of infection on the varieties, Collins and Mann.

These differences have been utilized in measuring the relative susceptibility of aecidial hosts. Thus, members of the apple family may be separated into five groups which are defined as follows:

1. *Immune*. Plants which after inoculation show no visible symptoms of infection.

2. *Very resistant*. Plants on which flecks are the only symptom of infection.

3. *Resistant*. Plants on which the formation of pyrenidia occurs, but no aecidia develop.

4. *Susceptible*. Plants which are resistant commonly but on which aecidia develop rarely or in limited numbers.

5. *Very susceptible*. Plants on which aecidia form commonly and in large numbers.

Of the plants which show symptoms of infection, only the susceptible and very susceptible ones act as alternate hosts to the rust. It is only through them that the pathogene can complete its life cycle.

EXTENT OF LOSS FROM LEAF SPOTS ON APPLES

Relative susceptibility is a qualitative value which depends on the nature of the host and parasite. The extent of loss from the disease due to destruction of leaf tissue is, on the other hand, a quantitative value, which depends primarily upon the number and size of lesions per unit area. Variations in values of relative susceptibility and the extent of loss, although showing agreement in certain situations, may fluctuate independently.

The infection scale³ illustrated in fig. 12 was prepared by tracing with a pencil about the margin of an apple leaf on a piece of cross section coordinate graph paper. The smallest squares on the paper measured 1 mm. on a side. After cutting out the pattern of the leaf, the number of millimeter squares on it was counted. One percent of the squares was then filled in with ink, the spots representing lesions of cedar-apple rust of the size and shape found on leaves of Jonathan apple where the points of infection are numerous. The outline of the leaf and of the spots was then traced on drawing paper. Enough additional squares were then filled with ink to cover 3 percent of the area. The process was continued until the leaf had been traced seven times on the drawing paper and there had been obtained a series of scale classes equal to 1, 3, 5, 10, 20, 30 and 50 percent, respectively, of the leaf area covered by rust spots. The infection scale after being inked, was used for comparison with diseased

³ A method for measuring the extent of loss from cedar-apple rust due to destruction of leaf tissue was devised in the summer of 1928, previous to the first general survey in the nurseries. A similar method, derived independently, has been described recently by Tehon and Stout (52). For sake of uniformity, the methods used in this survey will be translated as far as possible in terms of Tehon and Stout.

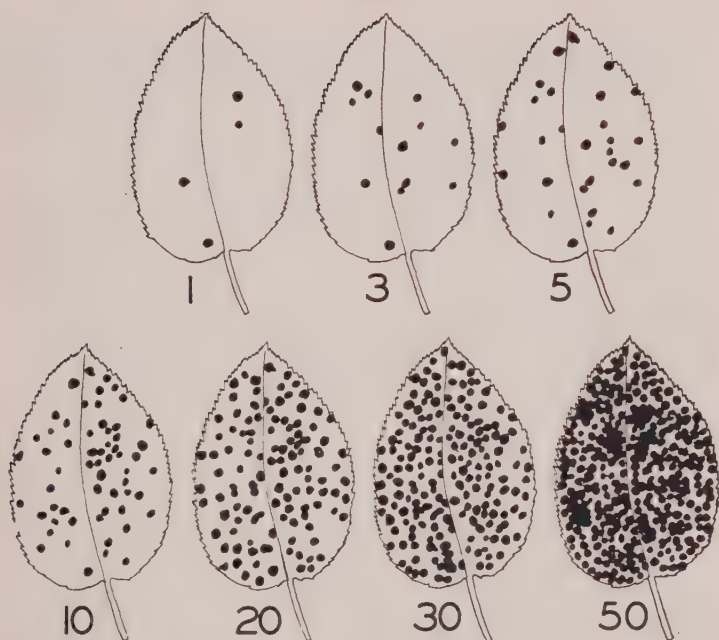


Fig. 12. An infection chart used for the purpose of judging the percentage of leaf area covered by lesions of cedar-apple rust.

leaves in estimating the percentage of area covered by rust lesions.

Data sheets were prepared on which were recorded all of the data for a single reading on the extent of leaf area rusted and the relative susceptibility of one variety of host at one location in the nursery. Another reading on the same variety, but at a different time or in another location, required a separate data sheet. The first survey was made in 1928 on a 40-acre block of "2-year-cut-back" apple trees which contained 49 varieties. The trees were growing in rows of 42 inches in width and stood about 6 to 8 inches apart. They measured from $\frac{1}{2}$ to 1 inch in caliper and stood from 4 to 7 feet in height.

Readings were taken in the following manner: A tree was selected according to a uniform procedure, namely, the first tree to be examined stood 25 paces from the end of the row. All of the leaves showing symptoms of rust were picked and placed in a paper sack, and their number was recorded on the data sheet. The rust-free leaves which remained on the tree were then counted. The next plant to be examined was the twenty-fifth tree from the first standing in the same row. All of the rusted leaves on it were counted and placed in the same sack. Because of the amount of labor involved, the number of healthy leaves remain-

ing, after removing the diseased ones, was counted on the first, fifth, tenth, fifteenth and twentieth trees examined. A reading included data from 20 trees. The numbers of diseased and healthy leaves had been written on the data sheet and all of the diseased leaves had been collected in one paper sack.

Further notations were made in the laboratory. If the number of diseased leaves exceeded 100, the leaves were shuffled and 100 were taken out at random. The additional leaves were discarded. Each of the hundred leaves was compared with the infection scale, already described, and sorted into one of seven groups according to the scale classes. When the sorting was completed, sometimes there were seven groups, one for each of the seven scale classes, but often there were fewer. The number of leaves in each scale class may be termed the "scale frequency" while the product of a scale class by its scale frequency may be called the "class value."

Table VII represents a typical data sheet which contains an actual reading on the Bayfield variety on July 23, 1928. The sum of the class values is 1,687 percent, giving an average of 16.87 percent. Variations in leaf area are not considered in making this calculation. With this restriction, it may be said that 16.87 leaves have the same total area as do the rust spots on the hundred sample leaves. By multiplying this average percentage by the average number of rusted leaves per tree, 88.45, a number of leaves is obtained, 14.92, representing, for the average tree, the total area on the rusted leaves which is covered by spots. This number is then divided by 309.2, the number of leaves on an average tree, to obtain the percentage of leaf area of an average tree covered by rust spots. In this case it is 4.82 percent.

Most of the infection on trees surveyed in 1928, had come evidently from 11 large red cedars. Nine of these were in a wind-break on the east side of the field and two stood near the southwestern corner. All of the red cedars were loaded heavily with galls of *Gymnosporangium juniperi-virginianae*.

The survey of 1929 included nine blocks of grafted and budded apple trees. The number of varieties was increased three times over that of 1928, and in addition, several readings were obtained on each of the more common sorts. Trees ranging in age from first year grafts to "2-year-cut-backs" were examined. In making the readings, the same procedure was followed as in 1928, except that 10 trees were used in a reading instead of 20 and the number of healthy leaves was counted on the first, fifth and tenth. The survey was made between Aug. 15 and Aug. 27.

Starting Aug. 7, 1930, and continuing until Aug. 25, readings were taken on about 175 varieties of apples and crab in nine nursery blocks. At the end of the survey there were from one to nine readings on each of the varieties, depending on the number of blocks in which each had been planted. In the places

TABLE VII. A TYPICAL DATA SHEET AS USED IN THE CEDAR-APPLE RUST SURVEYS, 1928 TO 1930, INCLUSIVE.

CEDAR-APPLE RUST SURVEY—1928

Variety: *Bayfield* Date: *July 23* Location: *South Farm, Block III, Row 146, Specimen No. 30*

Tree no.	No. diseased leaves	No. healthy leaves	Total leaves on tree	Percentage of leaf area rusted						
				(Scale classes)						
				1	3	5	10	20	30	50
1	122	260	382	(Class frequency)						
				19	6	10	16	21	19	9
2	80			(Class values)						
3	46			19	18	50	160	420	570	450
4	60			Sum of class values: 1,687 percent.						
5	90	223	313	Average: 16.87 percent, or .1687						
6	76			Average number rusted leaves per tree:						
7	58			$\frac{1769}{20} = 88.45 \text{ leaves.}$						
8	123			Average number total leaves per tree.						
9	120			$\frac{1546}{5} = 309.2 \text{ leaves.}$						
10	86	200	286	Total area rusted on average tree:						
11	85			$(.1687)(88.45) = 14.92 \text{ leaves.}$						
12	95			Total area rusted as a percentage of total						
13	109			leaf area (healthy plus diseased):						
14	84			$\frac{(100)(14.921515)}{309.2} = 4.82 \text{ percent.}$						
15	67	180	247	Symptoms:						
16	102			Lesions 2 to 5 mm. diam., occasionally 12						
17	78			mm. when separated widely, yellowish-						
18	108			orange to greenish, centers die prematurely;						
19	102			pycnidia many, 10-20; aecidia many and						
20	78	240	318	prominent, functional; leaves often necrotic						
				between spots and at tips; stem cankers						
				formed.						
Total	1769		1546							

where 2-year-old trees or scion orchard trees were examined, the diseased and healthy leaves were counted on one limb rather than on the whole tree. Besides expediting the work this method seemed to be nearly as accurate as the other.

The data on apples and crabapples obtained during the surveys of 1928 to 1930, inclusive, are summarized in table VIII. The varieties are divided according to their type of relative susceptibility and those in each type are arranged alphabetically. Where two readings were taken in a year, the percentage of rust is given for each. But in cases with more than two readings, only the lowest and the highest percentages are recorded. An abstract of notes on the symptoms of disease is included as a footnote to each group.

TABLE VIII. PERCENTAGE OF TOTAL LEAF AREA COVERED BY LESIONS AND THE SYMPTOMS OF DISEASE CAUSED BY *GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE* ON VARIETIES OF CULTIVATED APPLES AND CRABAPPLES AS SHOWN BY SURVEYS.

Variety	Percentage leaf area rusted								
	1928			1929			1930		
	No. of readings	Low %	High %	No. of readings	Low %	High %	No. of readings	Low %	High %

CULTIVATED APPLES

Very susceptible varieties:1

Adel*				1		1.02			
Bayfield	1		4.82	1		.7	2	.29	2.61
Benoni	1		3.71	3	.017	.426	6	.14	1.74
EdgeWood				1		1.58	2	.567	1.38
Goldo				1		.38	2	.811	1.39
Hightop June				3	.003	.705	2	.362	1.161
Iowa Blush				1		.222	3	.273	4.96
Jonathan	1		3.409	7	.15	2.46	9	.206	3.403
Large Red Romanite				1			1		.99
Minkler				1		1.138	2	.056	3.88
Missouri Pippin	1		1.99	2	.094	.188	2	.69	.856
Peter				1		.55	1		3.2
Red Canada				1		.59	1		.206
Red June	1		3.08	6	.006	1.943	8	.108	2.94
Rome	1		3.53	4	.002	.141	2	2.23	2.74
Red Rome Beauty				1		.225	2	.51	.83
Scott							2	.934	1.88
Twenty Ounce	1		3.68	5	.128	2.408	3	1.14	3.96
Wealthy	1		3.63	7	.037	2.26	7	.96	5.0
Yellow Bellflower	1		5.89	2	.236	.371	5	.517	2.486

Susceptible varieties:2

Bailey Sweet				2	.003	.063	2	.709	1.138
Cox Orange				1		.004	1		.078
Domine				1		.141	2	.4	.69
Dudley	1		.95	4	.002	.082	3	.15	.29
Early Strawberry				1		.207	1		.2
Erickson				3	.001	.112	3	.09	.148
Golden Russet	1		.757	1		.019	2	.121	.16
Early Golden Russet				1		.02	1		.427
Golden Sweet				2	.19	.36	2	.109	.16
Grimes	1		.252	6	0	.024	6	.003	.108
Late Strawberry				3	.019	.06	2	.07	.525
Ontario				3	.049	.25	2	.623	.819
Opalescent				1		0	1		.076
Fatten	1		1.086	2	.028	.05	2	.37	1.12
Peerless	1		1.37	2	.035	.204	3	.215	.41
Price Sweet				2	.088	.025	4	.103	1.01
Red Wing							2	.385	1.33
Roman Stem				4	0	.059	3	.015	.153
Salome	1		2.208	4	.043	.377	2	.682	.92
Secor				1		.145			
Smokehouse							2	.086	.185
Tompkins King				2	0	.003	2	.048	.85
Willow							2	.38	1.008
Winter Banana	1		1.45	1		.217	3	.26	.48
Winter Sweet Paradise				3	.014	.762	2	.31	.81

TABLE VIII—CONTINUED

Variety	Percentage leaf area rusted								
	1928			1929			1930		
	No. of read-ings	Low %	High %	No. of read-ings	Low %	High %	No. of read-ings	Low %	High %
Resistant varieties:3									
Allen Choice				4	0	.004	2	.21	1.53
Anoka				1		0	2	0	.026
Antonovka				1			1		.072
Arkansas	1		.272	4	0	.061	3	.028	.111
Arkansas Black	1		.298	3	0	.001	3	0	.042
Ben Davis	1		.35	3	.0004	.051	4	.007	.38
Boiken				1		.025			
Bough				4	0	.065	3	.067	.263
Cortland				5	0	.06	4	.008	.18
Early Harvest	1		.036	5	0	.027	3	.003	.034
Early Joe				1		0	1		.023
Esopus							2	.031	1.04
Fall Pippin	1		.138	2	0	.008	2	.01	.042
Gano	2	.35	.527	5	0	.029	4	.006	.069
Gideon							2	.002	.011
Golden Delicious				2	.033	.094	3	.018	.29
Golden Winesap				4	0	.014	2	.021	.042
Haralson				5	0	.015	4	.005	.26
Hibernal				1		0	2	.014	.259
Hubbardston	1		.227	2	.001	.009	2	.004	.48
Huntsman				2		0	3	.01	.062
Ingram				2	.006	.046	4	.026	.37
King David	1		.151	3	0	.003	2		0
Lobo				1		.007			
Lowell				1		.038	2	.029	.074
Lowland Raspberry	1		.103	4	0	.047	2	.022	.156
McIntosh	1		.496	7	0	.098	4	.011	.202
Early McIntosh							2	0	.29
Maiden Blush	1		.656	5	.007	.06	4	.018	.208
Malinda	1		.35	5	0	.049	3	.004	.213
Milwaukee				1		0	2	.024	.158
Minnehaha							1		.068
Monona				1		.007			
Northern Spy	1		1.68	2	.092	.12	4	.022	.408
Red Northern Spy				1		.056	2	.17	.417
Okabena	1		.78	1		.01	2	.113	1.23
Oldenburg	1		.181	3	.016	.077	4	.068	.31
Paragon				1		0	3	.006	.069
Perkins				2	0	.013	2		.012
Pewaukee				2	0	.248	4	.028	.83
Pound Sweet				2	0	.018	2	.019	.4
Ralls	1		.258	3	.011	.077	2	.026	.809
Rambo				4	0	.072	4	.025	1.9
Ramsdell Sweet				3	0	.012	4	0	.113
Red Astrachan	1		.188	5	0	.027	4	.01	.075
Red Duchess				2	.002	.053	2	.049	.59
Daniel's Red Duchess							1		.222
Rhode Island Greening				2	.017	.049	2	.016	.24
Roxbury				1		.01	2	.004	.053
Saint Lawrence				1		.006	1		.126
Stark	1		.93	1		.033	2	.011	.276
Stayman	1		.38	5	0	.022	4	.011	.312
Tetofski				3	.001	.095	2	.15	.26
Tolman	1		.33	5	0	.03	3	.002	.144
Turley				3	.012	.031	2	.041	.133
Utter				1		.005	2	.016	.156
Wagener	1		.595	2	.004	.055	3	.58	.111
Westfield				2	.00006	.014	2	.015	.072
White Pearmain							2		.025
Windsor Chief							2	.004	.045
Winesap	1		.303	4	0	.083	4	0	.077
Yellow Newtown							1		.211
Yellow Transparent	1		.422	7	0	.163	4	.062	.339
York Imperial	1		.317	4	.01	.083	4	.045	.195

TABLE VIII—CONTINUED

Variety	Percentage leaf area rusted								
	1928			1929			1930		
	No. of readings	Low %	High %	No. of readings	Low %	High %	No. of readings	Low %	High %
Very resistant varieties:4									
Ames				2	0	.002	2	.005	.016
Anisim	1		.089	1		0	2	0	.061
Baldwin				3	0	.032	4	.004	.103
Chenango				2	.004	.029	2		0
Chester White							1		.108
Delicious	1		.087	5	0	.005	4	0	.09
Fameuse	1		.139	3	0	.014	3	.004	.033
Gravenstein	1		.199	4	0	.014	4	.007	.049
Banks Red Gravenstein				2	.012	.028	1		.016
Hawkeye Greening				3	0	.071	2	.006	.008
Longfield				3	0	.049	2	0	.002
McMahon				1		.004	2	0	.012
Northwestern Greening	1		.025	4	0	.017	4	.005	.037
Richard				2	.002	.005	2	0	.009
Sharon				3	0	.013	2	0	.075
University							1		.022
Wisconsin Russet	1		.137				2	0	.049
Wolf River	1		.14	3	0	.011	2	.011	.019

Immune varieties:5

Collins						2	0
Mann						1	0

CRABAPPLES

Very susceptible varieties:

Red Siberian			2	.115	.164	3	.055	1.86
Sugar						1		.25
Whitney	1	2.091	6	.054	.88	9	.258	2.829

Susceptible varieties:

Red Tip				3	.032	.256	2	.024	.119
Sweet Russet				2	0	.12	2	.003	.004

Resistant varieties:

Florence			4	.002	.286	2	.128	.384
General Grant			1			1		.01
Hyslop	1	.9	3	.034	.177	2	.122	.27
King			1		.005	2	.061	.102
Martha			2	.019	.144	3	.245	.68
Minnesota			1		.003	2	.008	.048
Success			1		0	2	0	.005
Transcendent			2	.002	.022	2	—	.011
Virginia			2	.001	.041	3	.003	.76
Yellow Siberian			2	.038	.039	4	.034	.409

Very resistant varieties:

Cathay			1		.0005	1		0
Dolgo			2	.003	.012	2	.003	.08
Hopa			4		0	2	0	.013
Jumbo			1		.001			
Magnet						1		.02
Shields						1		.094

TABLE VIII—CONTINUED

Immune varieties:

Beauty			2		0	2		0
Dr. Van Fleet			2		0	2		0
Mercer County			1		0	1		0
Olga						2		0
Silver						1		0
Niedzwetzkyana			3		0	2		0
Red Vein			2		0	1		0

* Standardized nomenclature as set forth by Ragan (40, 41), Beach (8), and Close (16, 17, 18, 19, 20, 21) has been followed in this list.

1 *Very susceptible varieties*: Lesions on leaves 1 to 19 mm. diam., green, yellow, orange, or brown colored with numerous intergradations and margins commonly blotched with red or purple; pycnidia usually many, 1-25 per spot; aecidia many, functional; necrosis within or between lesions common in some varieties, lacking in others; stem cankers formed occasionally.

2 *Susceptible varieties*: Lesions on leaves fleck-like to 8 mm. diam., chlorotic green, yellow, orange or brown, often with reddish margins; pycnidia formed commonly, 1 to many per spot; aecidia present but not common, often rare due to early necrosis of the tissue; stem cankers formed occasionally.

3 *Resistant varieties*: Lesions on leaves from tiny flecks to 8 mm. diam., chlorotic green, yellow, orange, buff or brown colored, often inconspicuous; pycnidia 1 to 6 per spot but rare in some varieties; functional aecidia absent, swellings formed occasionally; premature necrosis of tissue seems to inhibit full development of fungus in many cases; stem cankers not observed.

4 *Very resistant varieties*: Lesions fleck-like, diameter 1 mm. or less, chlorotic green to dull yellow, often with necrotic centers; pycnidia and aecidia absent.

5 *Immune varieties*: No visible symptoms of infection.

It will be noticed that all degrees of susceptibility are exhibited. Among the varieties of apples, 20 are very susceptible, 25 are susceptible, 73 are resistant, 18 are very resistant and 2 are seemingly immune. Of the crabapples, 3 are very susceptible, 2 are susceptible, 10 are resistant, 6 are very resistant and 7 are immune.

A type of susceptibility not indicated above has been discerned in the case of the varieties, Patten Greening, Northern Spy, Okabena, Winter Banana, Stayman and Hyslop. The strain of rust at Shenandoah exhibits considerable virulence when attacking these varieties as is shown by the occasional formation of aecidia on Patten Greening and Winter Banana. But its development is checked prematurely by necrosis of the host tissue about the mycelium. Being unable to live in dead tissue, the rust is killed. The extent of injury which results is sometimes negligible, although if all of the varieties are considered, the damage is approximately equal to that found on the susceptible sorts. The reaction of these hosts is similar to the second type of disease resistance noted by Reed and Crabill (44) and also to the hypersensitiveness described by Stakman (47) in connection with *Puccinia graminis*. It has not been used in judging susceptibility because it overlaps other types and is a phenomenon which is not easily determined.

The chlorosis of tissue surrounding rust lesions is apparently a secondary symptom of the disease. When infection is severe and the relative humidity is low, a situation found commonly

in 1930, necrosis follows shortly after chlorosis. The very susceptible varieties of apples are particularly affected with necrosis on the leaves between the spots and also at the margins. With some varieties, the centers of the spots die and drop out following the formation of pyrenidia.

Gymnosporangium juniperi-virginianae, unlike many leaf-spotting fungi, is not capable of secondary infection from one apple leaf to another. Because of continued vegetative growth of trees in the nursery, a considerable portion of the leaves may escape infection. Orchard trees are more seriously affected under the same conditions because a larger percentage of the leaves are present during the infection period. Also, because the fruit is attacked.

RELATION BETWEEN THE PERCENTAGE OF LEAVES INFECTED AND THE
EXTENT OF LOSS

During the life of each apple leaf there seems to be a period of susceptibility to cedar-apple rust after which immunity develops. Miller (36) succeeded in inoculating old leaves of susceptible varieties through tears in the epidermis, indicating that such leaves owe their resistance to some change in the epidermis.

Data from 1928 have been used in table IX to illustrate how

TABLE IX. A COMPARISON OF THE PERCENTAGE OF RUSTED LEAVES WITH THE PERCENTAGE OF TOTAL LEAF AREA RUSTED AND THE RELATIVE SUSCEPTIBILITY OF 49 VARIETIES OF APPLES IN THE SURVEY OF 1928.

Variety	Per-centage rusted leaves	Per-centage total leaf area rusted	Susceptibility*	Variety	Per-centage rusted leaves	Per-centage total leaf area rusted	Susceptibility*
Salome	51.1	2.208	S	Malinda	18.3	.35	R
Wealthy	50.95	3.63	VS	Ben Davis	17.8	.35	R
Rome	47.7	3.53	VS	Okabena	17.66	.78	R
Yellow Bellflower	44.0	5.89	VS	Tolman	17.3	.33	R
Twenty Ounce	39.44	3.68	VS	Patten Greening	17.2	1.086	S
Jonathan	37.8	3.409	VS	Stayman	16.6	.38	R
Winter Banana	37.5	1.45	S	York Imperial	16.2	.313	S
Northern Spy	33.6	1.68	R	Grimes	15.9	.252	S
Red June	32.8	3.08	VS	Red Astrachan	15.7	.188	R
Whitney	32.8	2.09	VS	Hubbardston	15.5	.227	R
Missouri Pippin	31.28	1.99	VS	King David	15.1	.151	R
Bayfield	28.6	4.82	VS	Winesap	14.9	.303	R
Benoni	27.7	3.71	VS	Arkansas Black	14.8	.298	R
Peerless	27.7	1.37	S	Arkansas	14.0	.271	R
Hyslop	26.5	.9	R	Fameuse	13.9	.139	R
McIntosh	25.8	.496	R	Fall Pippin	13.8	.138	R
Golden Russet	25.06	.757	S	Wisconsin Russet	13.7	.137	VR
Maiden Blush	24.36	.656	R	Oldenburg	12.7	.181	R
Stark	23.3	.93	R	Wolf River	12.3	.14	VR
Ralls	21.5	.253	R	Lowland Raspberry	10.3	.103	R
Yellow Transparent	21.2	.422	R	Anisim	8.9	.089	VR
Wagener	21.04	.595	R	Delicious	8.4	.087	VR
Dudley	20.37	.95	S	Early Harvest	3.2	.036	R
Gano	19.45	.527	R	Northwestern			
Gravenstein	19.2	.199	VR	Greening	2.6	.025	VR

* VS = Very susceptible

S = Susceptible

R = Resistant

VR = Very resistant

the percentage of infected leaves compares with the percentage of rust on each variety. The varieties are listed in order accord-

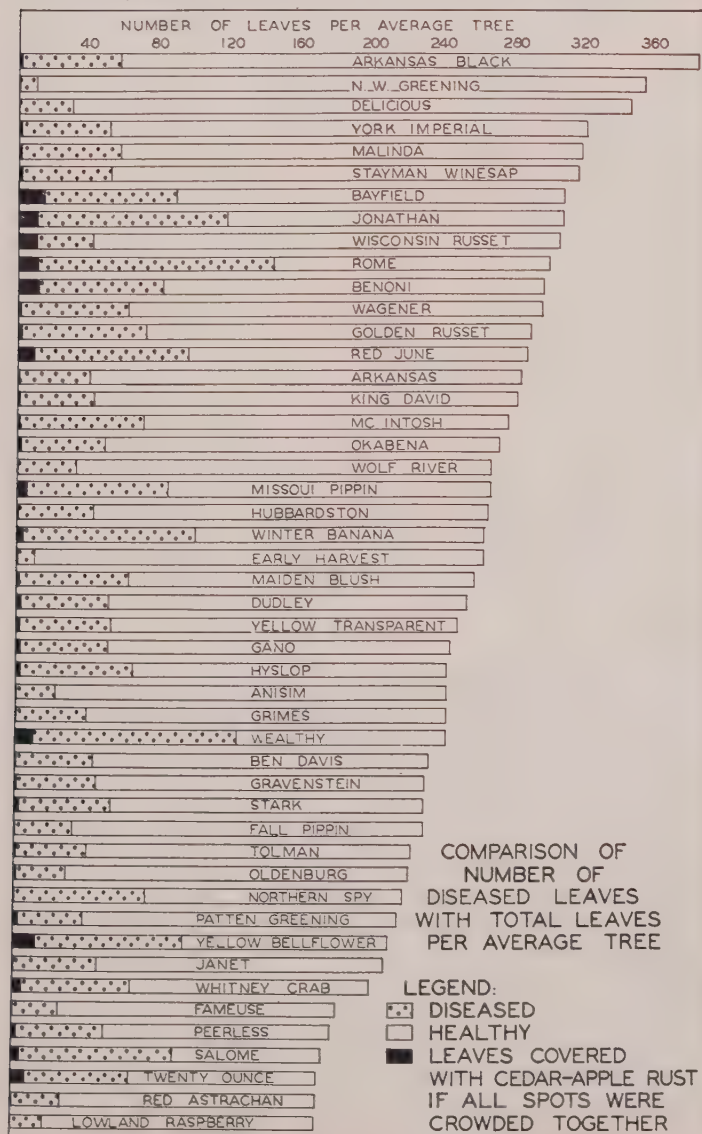


Fig. 13. Graph showing a comparison of the number of diseased leaves with the total leaves per average apple tree in the nursery.

ing to the percentage of rusted leaves. It will be seen that the trend in the second column is the same as in the first: the percentage of total leaf area rusted seems to vary roughly as the percentage of rusted leaves. There seems to be some agreement also between the percentage of rusted leaves and the susceptibility.

That these similarities are coincidental is not probable because they occur in data from other fields as well. To explain them by suggesting that the susceptible varieties had a larger percentage of leaves exposed during the infection period than did the resistant ones, is quite contrary to fact. In 1929 and 1930, observations showed that all varieties of apple in the nurseries were well leafed out before the period of maximum infection from rust. While it is not possible to explain the apparent relation between the percentage of leaves infected and the amount of rust, the evidence suggests that the period of susceptibility in leaves of very susceptible varieties is longer than that of very resistant ones. This theory, while not explaining the differences in susceptibility may, if further experiments were conducted, explain why leaves of some varieties avoid disease by passing quickly through the period of susceptibility. Figure 13 shows that in regard to the data of 1928, leafiness is not related to the amount of rust infection. Northwestern Greening and Delicious, two of the most resistant varieties known, produce nearly the largest number of leaves. The Twenty Ounce and Peerless varieties which are very susceptible have comparatively few leaves.



Fig. 14. Cankers of cedar-apple rust on stems of Wealthy apple.

OCCURRENCE OF STEM CANKERS

Of the 49 varieties examined in 1928, 19 were found with stem cankers. Pycnidia were found on all of these, but aecidia appeared only on seven. Rust infection is shown on stems of Wealthy and Yellow Bellflower in figs. 14 and 15. The varieties with stem cankers in 1928 are listed in table X. Cankers may cause considerable damage to young trees by forming points of weakness along the stems. If complete girdling occurs, the branch dies beyond the infection.

TABLE X. SURVEY OF 1928: VARIETIES OF APPLES WITH STEM CANKERS OF CEDAR-APPLE RUST.

Cankers with aecidial cups	Cankers with pycnidia only	
Yellow Bellflower	Benoni	Arkansas
Bayfield	Twenty Ounce	Red Astrachan
Wealthy	Jonathan	Wagener
Rome	Whitney	Malinda
Red June	Winter Banana	Stayman
Salome	Peerless	
Missouri Pippin	Okabena	

INHERITANCE OF DISEASE RESISTANCE

There are some indications that the factors for resistance are transmitted genetically. Table XI contains varieties of known parentage. The agreement between the progeny and one or both of the parents is evident in a number of cases. Since trees of one variety of apples are propagated vegetatively from one seedling, it is not possible by the use of these data to determine the



Fig. 15. Cankers of cedar-apple rust with many open aecidia on twigs of Yellow Bellflower apple.

manner in which disease-resistance is transmitted. The data indicate merely that the parents have influenced the susceptibility of their progeny toward cedar-apple rust in a number of cases.

TABLE XI. A LIST OF APPLE VARIETIES OF KNOWN PARENTAGE WITH NOTATIONS REGARDING THEIR SUSCEPTIBILITY TO CEDAR-APPLE RUST IN IOWA.

Progeny	Seed parent	Pollen parent
Edgewood (VS)	Salome (S)	Jonathan (VS)
Ontario (S)	Northern Spy (R)	Wagener (R)
Secor (S)	Salome (S)	Jonathan (VS)
Early McIntosh (R)	Yellow Transparent (R)	McIntosh (R)
Cortland (R)	Ben Davis (R)	McIntosh (R)
Monona (R)	Wolf River (VR)	Harrington
Ames (VR)	Allen Choice (R)	Perry Russet
Sharon (VR)	McIntosh (R)	Longfield (VR)
Olga Crab (I)	Oldenburg (S)	<i>Pyrus baccata cerasifera</i>
Bayfield (VS)	Malinda (R)	
Goldo (VS)	Grimes (S)	! Oldenburg (S)
Peter (VS)	Wealthy (VS)	
Dudley (S)	Oldenburg (S)	
Patten Greening (S)	Oldenburg (S)	
Red Wing (S)	Malinda (R)	
Anoka (R)	Mercer County Crab (I)	
Arkansas (R)	? Winesap (R)	
Haralson (R)	Malinda (R)	
Ingram (R)	Ralls (R)	
Lobo (R)	McIntosh (R)	
Milwaukee (R)	Oldenburg (S)	
Minnehaha (R)	Malinda (R)	
Okabena (R)	Oldenburg (S)	! Wealthy (VS)
Pewaukee (R)	Oldenburg (S)	
Stayman (R)	Winesap (R)	
Turley (R)	Winesap (R)	
Sugar crab (VS)	Antonovka (R)	
Cathay (R)	<i>Pyrus ringo</i>	
Dolgo (R)	<i>Pyrus baccata</i> (R)	
Beauty (I)	<i>P. baccata cerasifera</i>	
Red Vein (I)	Niedzwetzkyana (I)	
King David (R)	? Jonathan (VS)*	
Jonathan (VS)	? Esopus (R)	
Perkins (R)	? Malinda (R)	

* or ? Winesap (R)

Of the Russian varieties studied, eight were resistant and four were very resistant. Table XII summarizes readings on these for 3 years. The fact that all of the 12 Russian varieties were resistant over a period of 3 years may be of some practical significance.

TABLE XII. DISTRIBUTION OF READINGS ON SUSCEPTIBILITY OF 12 RUSSIAN VARIETIES OF APPLES TO CEDAR-APPLE RUST.

Variety	Number of readings					
	I	VR	R	S	VS	Total
Antonovka	1		1			2
Boiken			1			1
Hibernal	1		2			3
Lowland Raspberry	1	5	1			7
Oldenburg		1	7			8
Red Astrachan	1	6	3			10
Tetofski			5			5
Yellow Transparent	1	4	7			12
Anisim	2	2				4
Longfield	2	3				5
Dolgo crab		5				5
Beauty crab	4	1				5

RELATIVE SUSCEPTIBILITY OF OTHER HOSTS

Thus far the susceptibility of apples and crabapples to *G. juniperi-virginianae* has been considered. Other host plants include species of *Pyrus* and *Juniperus*. The aecidial hosts will be considered first.

AECIDIAL HOSTS

Pyrus ioensis (Wood) Bailey and its cultivated variety, Bechtel's double flowering crab, are without question the most susceptible aecidial hosts known in Iowa. The effect of infection

on the stems is shown in figs. 16 and 17. This species is the native flowering crab west of the Mississippi River which was earlier referred to *P. coronaria* L. One reading on 2-year-old trees of Bechtel's crab was made in 1928 where 44.9 percent of the total leaf area were rusted. This is nearly nine times the reduction in leaf area that was found on Yellow Bellflower, the most susceptible of the 49 varieties of apples growing in the same field. The survey re-



Fig. 16. Cankers of cedar-apple rust on stems and leaf buds of Bechtel's flowering crab.

vealed also that 75 percent of the leaves on Bechtel's crab were infected with rust as against 44 percent on Yellow Bellflower. This suggests that leaves of Bechtel's crab may remain susceptible to infection over a longer period of time than those of the apple.

But another difference is evident. Lesions on leaves of the crab are commonly 10 to 20 mm. in diameter, while those on the



Fig. 17. Defoliation, breaking over, and death of Bechtel's flowering crab in the nursery due to cedar-apple rust.

Bellflower apple are 2 to 13 mm. If an average spot on the crab is 15 mm. in diameter and that on the apple is 7.5 mm., the area of such spots, if they are circular, is 176.7 and 44.17 sq. mm., respectively. If, because of tolerance of the host, lesions on Bechtel's crab reach four times the area they do on apple, the difference in amount of leaf area destroyed is partially explained.

None of the species of *Pyrus* examined which have been introduced from Asia for ornamental, fruit, or breeding purposes, were found to serve as an alternate host of *Gymnosporangium*. Observations on the relative susceptibility of *Pyrus* spp., exclusive of *P. malus*, are given in table XIII.

TABLE XIII. OBSERVATIONS ON THE SUSCEPTIBILITY OF *PYRUS* SPP. (EXCLUSIVE OF *P. Malus*) TO *G. JUNIPERI-VIRGINIANAE* AT SHENANDOAH, IOWA, 1928-1930, INCLUSIVE.

Pyrus sp.	Observations		Remarks
	Year	Percent-age rust	
<i>P. ioensis</i> (including Bechtel's double-flowering crab)	1928	44.9	Very susceptible. Lesions large, commonly 10 to 20 mm. diam., orange to bright yellow or greenish yellow, often with trace of red, coalescing when crowded; pycnidia extremely numerous, commonly 50 to 200 per spot, later appearing in a ring about the margin, distinct, golden at first, later black; acidia formed in great numbers, commonly in a ring just outside the initial pycnidia; mycelium invades leaves, petioles, succulent stems, fruit and buds causing hypertrophy; cankers on stems and petioles cause necrosis in distal parts.
	1929	.95	
	1929	3.01	
	1929	4.4	
	1929	.703	
	1930	6.2	
	1930	9.07	
	1930	7.3	
	1930	8.84	
	1930	3.28	
	1930	6.06	
<i>P. baccata</i>	1929	0	Resistant. Lesions to 5 mm. diam., dull orange or brown, inconspicuous; pycnidia formed in small groups but no acidia or reverse swellings.
	1930	.06	
<i>P. spectabilis</i>	1929	.06	Resistant. Lesions mostly fleck-like or small; pycnidia formed occasionally; tissues die before acidia form.
	1929	.005	
	1929	.073	
	1930	.007	
<i>P. pulcherrima</i>	1930	.035	Very resistant. Necrotic flecks are only indication of infection.
	1928	trace	
	1928	"	
	1929	0	
	1930	0	
	1930	.018	

TABLE XIV—CONTINUED

<i>P. pulcherrima</i> var. <i>arnoldiana</i>	1928	trace	Very resistant. Flecks of uncertain origin.
	1929	0	
	1929	0	
	1930	.004	
	1930	.0052	
<i>P. pulcherrima</i> var. <i>scheideckeri</i>	1930	0	Immune.
<i>P. pulcherrima</i> var. <i>atrosanguinea</i>	1929	0	Immune for all practical purposes.
	1929	0	
	1930	.022	
	1930	0	
<i>P. halliana</i> var. <i>parkmanii</i>	1928	trace	Very resistant. Tiny necrotic points only.
	1929	0	
	1929	0	
	1930	trace?	
	1930	trace?	
<i>P. atropurpurea</i>	1929	0	Immune.
	1930	0	
<i>P. sargentii</i>	1928	0	
	1929	0	
	1930	0	

TELEUTOSPORE HOSTS

As far as has been determined, the only teleutospore hosts of the cedar-apple rust fungus in Iowa are *Juniperus virginiana* L. and *J. scopulorum* Sarg. The latter is an introduced ornamental, native in the Rocky Mountains. Bliss (10) failed to discover any galls of cedar rust on *J. scopulorum* during 1928. The hope arose that this western red cedar, also having a pyramidal, upright habit of growth, might be substituted for the common red cedar where cedar-apple rust is destructive. In 1929 galls of the disease, however, were found on *J. scopulorum* at Hampton, Charles City, Des Moines, Shenandoah and Ames. If the number of galls on a tree may be considered an indication of relative susceptibility, this variety seemed more resistant than *J. virginiana*.

The susceptibility of *J. virginiana* and nine of its grafted varieties was observed in the nurseries at Shenandoah for 3 years. Varieties, *elegantissima* Hochst., *canaertii* Senecl. and *glauca* Carr., were grown commonly and all were very susceptible to cedar-apple rust. Two trees of *J. virginiana* var. *keteleeri* Hort., were observed closely, but no rust galls of any kind developed. These trees stood within 30 feet of common red cedars which

during the same time were loaded with galls. The resistance of this variety was also noted by White,⁴ who after examining many trees found but one gall of *Gymnosporangium* and that was of *G. juniperi-virginianae*.

Figure 18 illustrates a small branch of red cedar which is severely infected with the disease. Notes on the susceptibility of species of *Juniperus* to cedar-apple rust in Iowa from 1928 to 1930, are summarized in table XIV.



Fig. 18. A branch of red cedar bearing many galls of *Gymnosporangium juniperi-virginianae*.

PHYSIOLOGIC SPECIALIZATION

During the cedar-apple rust survey of 1928, it became evident that on certain varieties of apples the pathogenicity of rust at Shenandoah was very different from that reported in the far eastern states. The York Imperial variety is mentioned by Reed and Crabill (44) and others as being very susceptible in Virginia where it is grown commercially. In Iowa this variety is distinctly resistant. Other varieties showing marked differences in susceptibility are Tolman, Ben Davis and Oldenburg.

Experiments which are reported in the following pages were undertaken to detect differences in the pathogenicity of various geographic strains of *G. juniperi-virginianae* and also of testing the susceptibility of apples from various states.

MATERIALS USED

For artificial inoculation in the greenhouse 2-year-old apple trees were obtained from five nurseries in three states.⁵ Numerous trees of apple, Bechtel's flowering crab, Amelanchier, Aronia, Cydonia and Pyrus were inoculated⁶ outdoors in nursery rows.

⁴ Unpublished correspondence, Richard P. White, New Brunswick, N. J., Sept. 8, 1930.

⁵ Apple variety	Obtained from
Tolman	Shenandoah Nurseries, Shenandoah, Iowa
Fameuse	Shenandoah Nurseries, Shenandoah, Iowa
York Imperial	Mount Arbor Nurseries, Shenandoah, Iowa
Yellow Transparent	Mount Arbor Nurseries, Shenandoah, Iowa
Tolman	Skinner Nurseries, Topeka, Kan.
York Imperial	Skinner Nurseries, Topeka, Kan.
York Imperial	Old Dominion Nurseries, Richmond, Va.
Bechtel's Flowering Crab	Snyder Bros. Nursery, Center Point, Iowa

⁶ Inoculum for experiments in the greenhouse and in the field was kindly contributed by the following: Dr. O. H. Elmer, Manhattan, Kan.; Mr. E. C. Mandentown, Dr. J. H. Muncie, and Mr. Boyer, Lansing, Mich.; Mr. Anthony Berg, Morgantown, W. Va.; Dr. R. E. Vaughan and Dr. A. J. Riker, Madison, Wis.; Mr. J. A. Evans, Poughkeepsie, N. Y.; Dr. E. F. Vestal and Mr. Wm. Overholt, Ames, Iowa; Dr. H. T. Güssow, Ottawa, Canada; and Dr. G. H. Berkeley, St. Catharines, Ontario.

TABLE XIV. SUMMARY OF READINGS ON THE SUSCEPTIBILITY OF *JUNIPERUS* SPP. TO *G. JUNIPERI-VIRGINIANAE* IN IOWA, 1928 TO 1930, INCLUSIVE.

Juniperus sp.	1928		1929				1930		
	Shenandoah	Ames	Charles City	Des Moines	Shenandoah	Ames	Shenandoah	Charles City	Ames
<i>J. virginiana</i> L.	+	+	+	+	+	+	+	+	+
<i>J. virginiana</i> var. <i>elegantissima</i> Hochst.	+	+			+		+		
<i>J. virginiana</i> var. <i>schottii</i> Gord.	+	+					+		
<i>J. virginiana</i> var. <i>globosa</i> Beiss.									
<i>J. virginiana</i> var. <i>canaertii</i> Senecl.	+	+	+		+	+	+		
<i>J. virginiana</i> var. <i>pyramidiiformis</i> D. Hill						+			
<i>J. virginiana</i> var. <i>hillii</i> Hort.		—							+
<i>J. virginiana</i> var. <i>keteleeri</i> Hort.	—				—				
<i>J. virginiana</i> var. <i>glauca</i> Carr.	+		+		+		+		
<i>J. virginiana</i> var. <i>burkii</i> Hort.							—		
<i>J. scopulorum</i> Sarg.	—	—	+	+	+	+	+	+	+
<i>J. communis</i> L.	—	—		—			—	—	
<i>J. communis</i> var. <i>evectica</i> Loud.	—	—			—		—	—	
<i>J. communis</i> var. <i>hibernica</i> Gord.	—	—			—		—	—	
<i>J. communis</i> var. <i>depressa</i> Pursh.	—	—			—		—	—	
<i>J. communis</i> var. <i>ashfordi</i> Hort.	—	—					—	—	
<i>J. chinensis</i> L.				—			—	—	
<i>J. chinensis</i> var. <i>pfitzeriana</i> Späth.	—	—					—	—	
<i>J. chinensis</i> var. <i>pyramidalis</i> Beiss.	—	—					—	—	
<i>J. chinensis</i> var. <i>sargentii</i> Henry	—	—					—	—	
<i>J. chinensis</i> var. <i>stricta</i> Hort.	—	—			—		—	—	
<i>J. chinensis</i> var. <i>columnaris</i> Hort.	—	—			—		—	—	
<i>J. excelsa</i> var. <i>stricta</i> Rollison	—	—			—		—	—	
<i>J. horizontalis</i> Moench.	—	—			—		—	—	
<i>J. sabina</i> L.	—	—			—		—	—	
<i>J. sabina</i> var. <i>tamariscifolia</i> Ait.	—	—					—	—	
<i>J. sabina</i> var. <i>horizontalis</i>	—	—					—	—	
<i>J. meyeri</i> (probably <i>J. squamata</i> var. <i>meyerii</i>)							—	—	
<i>J. volga</i> (ident. ?)							—	—	
<i>J. oblongata</i> (ident. ?)							—	—	

+ Infection.
— No infection.

METHOD OF INOCULATION

Three methods of inoculation were used in preliminary trials. The first consisted of suspending a sporulating gall over the moistened plant and covering the gall and plant with a bell jar. The second was to spray the plant with a suspension of sporidia in water, then cover the leaves with a wet paper sack. In the third method, leaves to be inoculated were moistened by atomizing with freshly distilled water. A spore horn was removed with forceps from a sporulating gall and rubbed or smeared over the leaves. A wet paper bag was then inverted over the branch, tied with string about the mouth and retained in place for about 48 hours.

Although infection was obtained successfully by the first method, it was wasteful of inoculum and plant materials. The second method was not successful. The third method was adopt-

ed for use both in the greenhouse and in the field because abundant infection could be obtained in a large percentage of cases, and only small amounts of teleutospore material were needed. Several branches on each of the larger trees could be inoculated at the same time with different collections of rust without danger of confusion.

GREENHOUSE TRIALS

By taking 2-year-old apple trees into the greenhouse between Jan. 23 and Jan. 28, 1930, it was possible to conduct inoculation experiments before any infection occurred out of doors. Cedar rust galls were obtained in a more or less dormant condition and were induced to sporulate in the laboratory. The inoculum which proved most satisfactory was that sent on a living tree from Morgantown, West Va. Several collections of immature galls from other localities became so dry during shipment that the spores could not be made to germinate.

In table XV are brought together the data obtained on the pathogenicity of five geographic strains of *G. juniperi-virginianae* on five aecidial hosts as shown by artificial inoculations in the greenhouse. Inoculum for all experiments was taken from *Juniperus virginiana*. The individual experiments are designated by letters. Inoculations were made between March 1 and April 19, 1930, and final readings⁷ were taken June 7. Untreated branches were held as controls in each experiment, but as no rust occurred on any of them, they are not included in the table.

The results obtained in these experiments indicate that the strain of cedar-apple rust from Morgantown, W. Va., was more virulent than those from Iowa, Kansas and Wisconsin. This was shown by the aecidia produced on the varieties Tolman and York Imperial by the West Virginia strain, whereas the other collections produced only flecks or a few pycnidia. Rust from Ames and Shenandoah caused the development of disease symptoms which are comparable with those resulting from natural

⁷ Certain explanatory notes, too long to be included in table XV, are indicated by numbers. These notes follow:

- (1) Partially formed pycnidia found. Dead.
- (2) Two pycnidia.
- (3) A few dead pycnidia.
- (4) A few pycnidia formed singly.
- (5) Necrotic circular areas, 1 to 4 mm. in diameter.
- (6) Flecks and necrotic spots.
- (7) One leaf with many circular necrotic spots. Points of infection from rust show as small necrotic specks.
- (8) Six pycnidia formed. All dead.
- (9) A single pycnidium formed.
- (10) Strong swellings on lower surface of lesions.
- (11) Strong swellings on lower surface of lesions.
- (12) Many pycnidia formed; slight reverse swelling.
- (13) Pycnidia and strong reverse swellings formed.
- (14) Limb broken off after being inoculated.
- (15) Many flecks, all with necrotic centers.
- (16) Slight flecks, leaves old when inoculated.
- (17) Many pycnidia and aecidia; infection heavy.

TABLE XV. PATHOGENICITY OF FIVE GEOGRAPHIC STRAINS OF *G. JUNPERI-VIRGINIANAE* ON FIVE AECIDIAL HOSTS AS SHOWN BY ARTIFICIAL INOCULATIONS IN THE GREENHOUSE.

Host	Source of host	Source of inoculum																							
		Ames, Iowa						Shenandoah, Iowa						Manhattan, Kan.						Morgantown, W. Va.					
		Experiment						Experiment						Experiment						Experiment					
		A	B	E	I	L	O	S	Y	D	K	Q	T	Z	G	M	N	U	C	J	P	R	W		
Fameuse	Iowa	0 ^a	0	0	0	—	0	0	0	0	—	0	0	0	0	—	0	0	0	0	0	0	0	X	
Tolman	Iowa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	□	X	0	0	0	0	
Tolman	Kans.	0	0	0	0	0	0	(5)	0	0	0	0	0	0	0	—	0	0	0	X	(11)	0	(15)	0	
Yellow Transparent	Iowa	0	0	0	0	0	0	(6)	0	0	0	0	0	0	0	—	0	0	0	0	X	0	(16)	0	
York Imperial	Iowa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	0	0	0	
"	Kans.	0	X	0	X	0	0	0	0	0	0	0	—	0	0	0	0	0	X	X	X	0	0	0	
"	Va.	(1)	0	X	(3)	0	0	(7)	0	—	0	0	0	0	X	(8)	—	0	□	(10)	(13)	0	0	0	
Bechtel's Flowering Crab	Iowa	□	(2)	□	□	□	□	(4)	0	—	0	0	0	0	0	—	0	0	□	□	□	0	0	0	
									X	—	0	□	—	X	□	—	X	0	—	X	(14)	—	(17)	—	

* Legend: — No signs of infection

0 Flecking

X Pycnidia

□ Aecidia

infection in Iowa. The Kansas strain was similar to the Iowa collections in virulence. From experiment X, it seems that cedar-apple rust from Cochrane, Wis., was less virulent than the other strains because it produced no disease on Bechtel's crab. As will be shown later, however, a similar collection caused heavy infection with pyrenidia and aecidia on Bechtel's crab at Shenan-

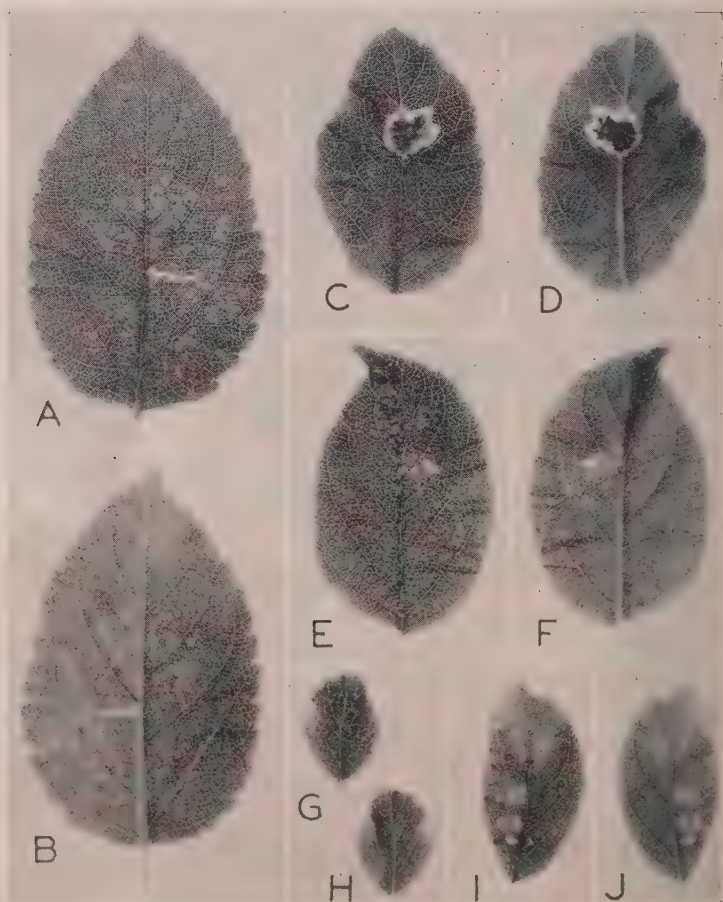


Fig. 19. Symptoms of cedar-apple rust on leaves of the variety, York Imperial. A-B. Inoculated with rust from Cochrane, Wis. C-D. inoculated with rust from Morgantown, W. Va. E-F. Inoculated with rust from Ames, Iowa. G-H. Inoculated with rust from Manhattan, Kans. I-J. Inoculated with rust from Shenandoah, Iowa.



Fig. 20. Symptoms of cedar-apple rust on leaves of the variety, Tolman. A-B. Inoculated with rust from Shenandoah, Iowa. C-D. Inoculated with rust from Cochrane, Wis. E-F. Inoculated with rust from Manhattan, Kans. G-H. Inoculated with rust from Ames, Iowa. I-J. Inoculated with rust from Morgantown, W. Va.

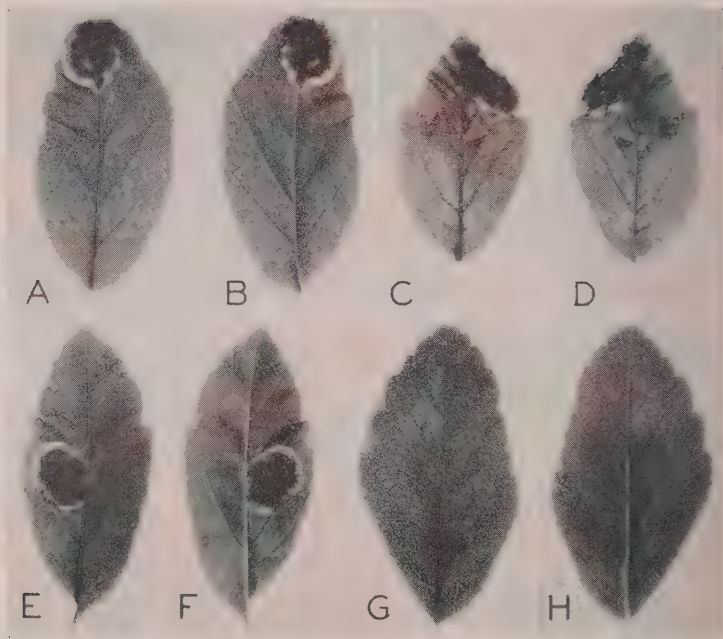


Fig. 21. Symptoms of cedar-apple rust on leaves of Bechtel's flowering crab. A-B. Inoculated with rust from Ames, Iowa. C-D. Inoculated with rust from Shenandoah, Iowa. E-F. Inoculated with rust from Manhattan, Kans. G-H. Inoculated with rust from Morgantown, W. Va. In experiment W this strain of rust produced many pycnidia and acedia on Bechtel's flowering crab. It may be considered that the symptoms pictured here do not indicate the actual pathogenicity of this rust.

doah. That the inoculum used in the greenhouse was viable in most cases is evidenced by the flecking it caused on inoculated leaves.

No consistent difference in susceptibility was found between trees of Tolman from Iowa and Kansas or between trees of York Imperial from Iowa, Kansas and Virginia. As far as these experiments are concerned, there is little to support the suggestion of Weimer (56) that there may be a variation in the susceptibility of apples in the various states.

While the strain of rust from West Virginia caused the formation of pycnidia and slight reverse swellings on Yellow Transparent and, at the same time, the other strains produced only flecking, the differences in pathogenicity are not great enough to warrant consideration. Also on Fameuse, no differential re-

action occurred. In these trials, the evidence which suggests physiologic specialization in *G. juniperi-virginianae* is therefore centered upon the marked difference in susceptibility of Tolman and York Imperial to the various strains. Proof of the viability of each strain rests upon its ability to produce aecidia on Bechtel's crab. Figures 19 to 21 picture the reaction of the five geographic strains on the varieties Tolman, York Imperial and Bechtel's crab, in experiments, B, Q, G, C and X.

FIELD TRIALS

Inoculations were made on plants found growing in nursery rows at Shenandoah. The results were somewhat less satisfactory than those from the greenhouse trials because of natural infection which occurred during the experiment. Each inoculation included either two or three plants, and the readings were made with control plants for comparison. In most instances, the inoculation caused such an abundance of infection, developing at one time, that it could be distinguished from that which occurred naturally. Table XVI gives the results of the experiments. The inoculi from Mason City, Iowa, and Morgantown, W. Va., were not very viable when used. It should be noted that Bechtel's crab was very susceptible to rust from Cochrane, Wis., in experiment DD. This inoculum was from the same source as that of experiment X, already mentioned, where Bechtel's crab was not infected.⁸

In comparison with the infection produced by the local strain, the only result of note is that in which rust from St. Catharines, Ontario, Canada, formed pycnidia on Delicious. This type of infection, however, was found only on one leaf. The result should be verified before making positive statements, but it is unique in being the only case where pycnidia of rust have been observed on this variety in Iowa.

⁸ Additional information concerning certain readings in table XVI follows:

- (18) Pycnidia formed in small groups but not of vigorous growth.
- (19) Extremely heavy infection.
- (20) Extremely heavy infection.
- (21) No results. Foliage in unthrifty condition.
- (22) Chlorotic flecking.
- (23) Flecks yellowish, later becoming purplish. A few isolated pycnidia.
- (24) A few dead pycnidia.
- (25) These scattering small lesions with pycnidia may possibly be from natural infection. Only five such lesions, however, were found on 100 uninoculated trees in the same row.
- (26) Eight small lesions with pycnidia on one leaf. The tree was similar to other plants in the row. This is the only known occurrence of pycnidia on Delicious in Iowa.
- (27) One lesion with pycnidia; the others only flecks.
- (28) Artificial infection certain. Many pycnidia found on June 31. No later reading made.

THE PATHOGENICITY OF *G. GLOBOSUM*

A single instance of resistance to *G. globosum* was discovered in a tree resembling *Crataegus crus-galli* L., while numerous other collections of *Crataegus* spp. taken at Shenandoah and Center Point, Iowa, were all very susceptible. Results from artificial inoculations⁹ in 1930 using four geographic strains of *G. globosum* on 15 pomaceous plants are given in table XVII. Preliminary inoculation experiments produced necrotic flecks on leaves of Baldwin, Tolman and Northwestern (Greening apple while no symptoms appeared on Wealthy, Early Harvest, Ben Davis and Benoni.

⁹ The following notations refer to certain readings in table XVII:

- (1) No results. Foliage in unthrifty condition.
- (2) Flecks very uncertain.
- (3) Thirty-five small lesions each with a single pycnidium on one leaf. Control plants free from similar symptoms.
- (4) These small, scattered lesions bearing pycnidia may be due to natural infection by *G. juniperi-virginianae*. However, only 5 such lesions were found on 100 uninoculated trees in the same row.

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